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The distribution of *Padina pavonica* (L.) Lamour. (Phaeophyta : Dictyotales) on British and adjacent European shores

James H. Price, Ian Tittley and
Walter D. Richardson

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The distribution of *Padina pavonica* (L.) Lamour. (Phaeophyta : Dictyotales) on British and adjacent European shores

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Synopsis

Padina pavonica is one of the few British marine algae for which there is a sufficiently long history of data, *relatively* plentiful and reliable, to permit conclusions as to distributional variation in time and space. The species reaches its current northern limits along southern British and Irish shores; there is strong circumstantial evidence that past, maybe ephemeral, populations occurred considerably further north. Contraction in distribution range, possibly one aspect of periodic or irregular regional response to environmental changes at range periphery, seems generally indicated. There may have been similar contraction on adjacent shores of Netherlands, Belgium and northern France. British foci of distribution are Devon (the earliest recorded), Dorset, and the Isle of Wight. Analogous foci can be recognised along northern French shores. Gametangial plants seem currently to be very rare outside the Mediterranean; even in it, gametangia seldom develop on plants in the first 0·5 m of the infralittoral. On British and perhaps adjacent continental shores, *P. pavonica* appears rarely to grow below that depth and this may accentuate gametangial scarcity. Tetrasporangia are much more common than gametangia on Atlantic shores, occurring especially in July to September. Basal perennation and vegetative spread remain very important. Plants seem to appear slightly earlier in the year in Atlantic areas near the Mediterranean.

Introduction

Many past British and Irish records of benthic marine algae are unsupported by representative specimens. Generally, the earlier the records, and in more recent times the more common the species, the more likely is the lack of material. The delimitation beyond reasonable doubt of phasic or irregular peripheral changes in distribution (expansion or contraction in range) over time for any long-established species therefore requires that the plants be both conspicuous enough to have been frequently noticed in the past and so distinctive that statements made in even the sketchiest of published data, however early, can be confidently accepted as relating to that species. Few British algae of distributional interest, the northern or southern limit or some characteristic and unusual discontinuity occurring here, qualify under such stringent requirements as regards data from the distant past, although more are susceptible to analysis in terms of the last 70–80 years. Species such as *Asparagopsis armata*, *Bonnemaisonia hamifera*, *Colpomenia peregrina*, and the more recent *Sargassum muticum* have established here during that time; recognition of these events was comparatively easier since by then phycological knowledge was more extensive and generally more accurate than in past eras, and the invasion by alien species is often more spectacular than long-term variations in the long-established flora. Jones (1974) provides the most recent broad review of distributional and floristic changes in the British marine benthic flora; his examples, for reasons given above, are mostly from the 20th century and even then concern less the

variations or loss of species than the spectacular introductions. Jones refers to a few instances, such as the fluctuations and periodic absences of *Nemalion helminthoides* (Vell.) Batt. on Anglesey. There have been very few attempts to determine what changes have occurred, even within this century, in distribution of any species or genus over a wide geographical area and we have been unable to trace *any* detailed attempt to examine the situation for a particular species throughout its recorded history in the British Isles, although there has been generalisation on the subject. Those detailed comparisons that have been made (Price & Tittley, 1972 and in prep.; Edwards, 1975; Price *et al.*, 1977*a*, *b*) have dealt with the relationship of past to present floras of restricted areas (mostly counties).

During work on the Kent marine flora, two of us (J. H. P.; I. T.) became aware that, amongst the older-established British marine flora, one of the few good candidates for species-oriented study in distributional change at range periphery over recorded time is *Padina pavonica.** The only *Padina* species reported for the study area, *P. pavonica* has long possessed both an English name ('Turkey-feather alga') and, previously, a pre-Linnean name (*Fucus maritimus Gallopavonis pennas referens* of C. Bauhin, 1620 *et seq.*) that were unequivocal and of common usage.

General distribution and ecology

Padina pavonica, indeed the whole genus *Padina*, is overwhelmingly of warmer water affinities. *P. pavonica* reaches its present European northern limit of distribution on the coasts of southern England and southern Ireland, and on the adjacent French coasts (Fig. 1). Sporadically, there have been reports of finds to the north and east of the limits as currently recognisable. The body of the paper presents detailed examination of the present European Atlantic distribution and of all the available evidence on previous occurrence. No attempt has been made precisely to delimit the world distribution of *P. pavonica* because of taxonomic uncertainties concerning some earlier records.

In the Mediterranean, apparently the centre of its distribution, *P. pavonica* is exclusively an infralittoral alga, occurring over a wide depth range. Plants are present, often in considerable abundance, in depths from about 0 m down to 20 m; in some areas (e.g. the Straits of Messina), they continue down to at least 40 m. Ramon & Friedmann (1966) reported the alga from 0 to 2·5 m at various Mediterranean localities; Zavodnik (1977) regarded it as characteristic in the Adriatic upper infralittoral in semi-exposed and well-illuminated localities; Feldmann (1937) recorded it to 20 m in the Banyuls region. No systematic search for the alga has been made in the infralittoral around British and adjacent continental shores, although the frequency and extent of recent infralittoral studies in southern Britain would suggest that if *P. pavonica* were commonly present it would have been noted. In those areas, the vertical distribution of *Padina* apparently extends from shallow pools and damp areas just below MHWS into the shallow infralittoral, 0·5 m below MLWS. With one possible exception, for which the data do not provide information more precise than 'dredged in Plymouth near Duke rock', records have never been established along British and adjacent continental coasts from greater depths. If this is a true, rather than an apparent, vertical amplitude, the constraints may lie with available light or with temperature levels (cf Liddle, 1975; Allender, 1977*a*, *b*). In Britain, the most prolific growth of this alga has been detected in the lower littoral, either on very wet rock or similar surfaces, or in shallow pools.

* The latest *International Code of Botanical Nomenclature* (Stafleu *et al.*, 1978) recognises in its list of *Nomina Conservanda* (entry for *Padina* Adanson, Appendix III : 270) that the correct name to be applied to that species of *Padina* occurring along European shores is *P. pavonica*. The current British check-list (Parke & Dixon, 1976) continues to list the species as *P. pavonia* (L.) Lamour. Since both forms of the specific epithet are non-standard (not accepted forms of adjectives derived from *pavo*), that form first used by Linnaeus (*Fucus pavonicus*, *Spec. pl.* . . . : 1162, 1753) has to be accepted (Silva, *in litt.*, 12 Oct. 1977; Papenfuss, 1977). We diverge from the opinions of Drs Silva and Papenfuss only on the point of whether *pavonius* (*Syst. nat.*, ed. 10 : 1345, 1759) and *pavonicus* are distinct or variant forms. They, with Thivy (in Taylor, 1960 : 234–235), regard them as distinct, therefore accepting the authorities for the combination *P. pavonica* as (L.) Thivy in W. R. Taylor. By contrast, we regard them as variants of the same epithet; the combination is therefore here cited as *Padina pavonica* (L.) Lamour. (*Hist. polyp.* . . . 1816 : 304). Although virtually all relevant authors [for details see Silva, 1952 : 276] back to Adanson (1763 : 586) had clearly indicated their intention to recombine *Fucus pavonicus* L. in *Padina* Adanson or elsewhere, those prior to Lamouroux (1816) made their statements in such a way as not to meet the requirements of Article 33 of the *Code* (Stafleu *et al.*, 1978).

Most of the known British and continental localities are sheltered from the direct effects of south-westerly and westerly seas (there are exceptions in the Channel Islands, Atlantic southern France and, apparently, in Portugal); in many cases, they are in very sheltered bays. In the Mediterranean, *Padina* usually grows in detritus over flat or shallowly inclined surfaces, although (Ramon, *pers. comm.*) it is found directly attached on rock surfaces along the coasts of Israel. In Britain, *P. pavonica* is most frequently found on rocks covered by soft sediments, in which the basal portions of the plants are buried; these probably have some anchoring effect on the otherwise mobile detritus. Feldmann (1938) came to a similar conclusion regarding plants of the Banyuls area and it is true also for elsewhere in the distribution range. Plants have not been detected in Britain growing directly attached to hard rock surfaces. In many of the areas in which *Padina* occurs, softer rocks present have been eroded by wave-action, frost, and other agencies, but any ledges of harder rocks have more strongly resisted erosion. Where these harder ledges have a gentle slope, sediment has been deposited. *Padina* appears able easily to exploit this type of surface, on which few other macrobenthic algae seem to grow successfully. In pools, plants of *Padina* grow on similar substrata and may there be associated with a variety of small lower-shore algae. Norris (1972, unpublished)* observed certain areas of Bembridge Lagoon, Isle of Wight, where in small valleys of eroded softer substrata between more solid raised areas of mudstone there was generally patchwork absence (valleys) and presence (raised areas) of *Padina*. He therefore suggested that *P. pavonica* '. . . cannot easily cope with a shifting substratum'. Some degree of compaction of detritus does seem to be necessary for effective colonisation by *Padina*; early growth stages and embryo populations apparently tend to be susceptible to substrate movement. The compaction may derive, in the right circumstances, from the anchoring effect of *Padina* itself.

The flabellate fronds of *Padina pavonica* commonly die back *en masse* during the winter months in Britain, unlike many parts of the Mediterranean, where plants in good growth can be observed during most months of the year in all but the really shallowest of infralittoral populations, although die-back occurs in individual plants. Even in southern England, however, it is possible during milder winters to observe the reduced fronds throughout the whole of the adverse weather period. The total disappearance in more usual winter conditions is only apparent, being the result of a more drastic die-back to leave only consistently buried portions that perennate. If the exact position of a population is known, rhizomatous portions of *P. pavonica* may be readily detected during the winter in scrapings of sediment from the summer-growth location. Winter collecting in previous eras was certainly rare, but aside from that it is not entirely surprising that, previous to 1968, few authentic instances existed of recordings from British shores during the winter months. The only traced examples are the 1908–09 winter data from Weymouth, in Cotton's field notes (BM). The more usual pattern is exemplified by Norris (1972, unpublished), who indicated that he first detected growth at Bembridge, Isle of Wight, at the end of May, although plants may have been visible at an earlier date since observations were only commenced at this time. The Bembridge populations almost died back by the second week in October although, possibly due to lack of wave-action and a slightly higher temperature, plants growing in the laboratory persisted until the end of November. This accords with our field observations of persistent visible growth throughout milder winter periods, and with Cotton's earlier statements.

Life-history

Reproductive patterns, and perhaps therefore life-history in the field, appear to be incomplete or only very rarely complete on British shores. This seems to apply equally to the largest part of *Padina pavonica* distribution elsewhere. Norris (1972, unpublished) did not record gametangial plants from Bembridge, Lyme Regis, or Ladram Bay, although the former two yielded tetrasporic material. Williams (1905) stated, without further explanation, that during summers 1904 and 1905 he had detected '. . . but very few . . .' sexual plants of *Padina* in Dorset (Weymouth) and Devon (Torquay; Sidmouth). Carter (1927) detected only tetrasporic plants in *P. pavonica* at Ladram Bay, Chapman's Pool, Lulworth Cove and Nothe Rocks, Weymouth, but noted meiotic division, which

* We are indebted to W. F. Farnham, Portsmouth Polytechnic, for drawing our attention to this work.

implies a potentially normal life-history. By contrast, Umezaki & Yoneda (1962) and Allender (1977*a*, *b*) indicated the presence of occasional non-meiotic spores in *Padina* spp. This apparent incompleteness in British *P. pavonica* could be a phenomenon of superficial and insufficiently persistent observation at appropriate (possibly very short) periods and in appropriate places (? perhaps the infralittoral) rather than the reflection of complete absence of the gametangial phase from British shores. Indeed, there is some rather dated evidence of the existence of antheridial material, collected in September 1892 (Weymouth, BM slide 9535) and in September 1894 (Chapman's Pool, 9538; Sidmouth, 9539). These are the only traced authentic examples of gametangial material from British shores. Since culture methods have not been employed to complete the life-history, we have been unable to add more recent British records of antheridial or oogonial plants. We are certainly able to confirm field rarity in all commonly exploited ecological niches and seasons.

This situation provides an interesting parallel, in view of the confirmed gametangial rarity, with that detailed by Edwards (1973) for certain species of *Ceramium* in the northern parts of their distribution ranges, and mentioned in general terms for *Padina* by Thivy (1959), Umezaki & Yoneda (1962), Liddle (1971, 1972, 1975), Gaillard (1972, 1973), Fagerberg & Dawes (1973), and Allender (1977*a*, *b*). Edwards was commenting on Dixon's (1965) hypothesis of '. . . physiological expression of reproductive capacity . . .'; this suggests that sampling successively further from a centre of distribution of a species would initially detect general production of gametangial and sporangial material, grading through loss of gametangial and then sporangial production, to a terminal peripheral zone of solely vegetative material, all reproductive potential being inhibited and maintenance of populations depending on vegetative fragments or spores carried from areas nearer to the distribution centres. Edwards found that (a) he could produce in culture both male and female gametophytes from tetrasporophytes, using plants from the northern part of the range of *C. flabelligerum* J. Ag.; and (b) there appeared (rare) carposporophytic specimens in field material of *C. shuttleworthianum* (Kütz.) Silva, from two localities in the northern periphery of its range. The latter establishes the field occurrence, however spasmodic, of fertile gametophytes, which Edwards was also able to demonstrate in cultures isolated from one of the two localities (the other could not be tested further due to culture contamination). Edwards therefore expressed the view that, at least in the species tested and possibly in general terms, the constraints on realisation of reproductive (gametangial) potential are not entirely inbuilt and physiological but are imposed from without by the ambient environment. This constraint is not always complete as occasional carposporophytic specimens can be detected by detailed study. Fagerberg & Dawes (1973) examined down to organelle levels the morphology of gametophytes and sporophytes, from Florida, of *P. vickersiae*; there the gametophytes habitually develop during the period November to March, alongside sporophytes which are present throughout the year. Gametophytes and sporophytes were isomorphic to a very high degree, the only differences (the gametophyte possessing nucleoli and lacking osmiophilic globules) being interpreted by Fagerberg & Dawes as indicating more active growth in the gametophytes. Allender (1977*a*) noted considerable behavioural differences between sporophyte and gametophyte of *Padina japonica* Yamada, as well as pronounced differences in cell dimensions. Sporophyte cells were significantly larger and thicker-walled than those of gametophytes from the same locations on Oahu (Hawaii). Gametophytes never formed more than 7 % of the populations sampled and were usually fewer than 4 %, depending on time of year. Nevertheless, gametophytes grew faster than sporophytes in a temperature (20 °C) lower than area ambient; in extremely high light conditions; and in all levels of water movement, although they were more susceptible to being damaged or destroyed where the latter was appreciable. Possibly plants in more rapid active growth are more demanding as to environmental characteristics, leading to sterility in or eradication of the haploid state unless the environmental balance is entirely favourable. Quite what this means in terms of life-history is not clear and, as indicated by the authors, a great deal more ecological, physiological, and biochemical work is required. In general terms, data from Edwards, Fagerberg & Dawes, Allender, and others support the Dixon hypothesis, as do all traced data for *Padina* reproductive pattern in the present area. Although a zone of solely vegetative *P. pavonica* appears to be lacking at the range periphery here, the proportion of even tetrasporangial plants detectable is relatively small by comparison with

total numbers of plants examined and with Mediterranean proportions (see later); overwintering of bases, with subsequent vegetative growth from them are, as indicated, very important.

The decision on which period of the year is likely to yield most profitable field data on gametangia in southern British *Padina* is not easy. Ramon (1969*a*, *b* : 346) reported that *P. gymnospora* in Mediterranean Israel often produces gametangia immediately below the site of injury; this same effect was noted when lesions were made in cultured material. Since *P. pavonica* quite commonly disintegrates *in situ* in Britain, it may be that the time of maximum gametangial production should be looked for during the period when plants are disintegrating, or in geographical areas where thallus-wounding by detritus is maximal but not eradicatory, or both. The period of disintegration, [September–] October–November [–December] in most areas, is later (or earlier!) than algal collecting would usually be commenced. The effect in geographical areas where thalli are frequently wounded could occur at any time, but a rhythm of predisposition to production of gametangia may exist more or less in phase with the normal period of frond disintegration. There is little British evidence for this effect of tissue disintegration one way or the other, although the few known examples of gametangial (♂) material do derive from September collections (1892, 1894). Allender (1977*a*) made some interesting and relevant observations on *Padina japonica* in Oahu. Although he did not indicate connection on a cause/effect basis, he made it clear that the gametophyte, growing more quickly than the sporophyte under the influence of strong water movement and yet being more flimsy and therefore more easily torn in those conditions, was nonetheless at the highest of its very low percentage presence amongst the total population in winter (February; 7% of population). These observations support the suggestion that disintegration or damage may accentuate the production of gametangia by the gametophyte. Fagerberg & Dawes (1973), working with Flordia plants of *P. vickersiae* from two sites and depths of 3 m and 1–2 m respectively, found field gametophytes (all dioecious) only from November to March. No mention was made of any connection with wounding or disintegration.

Previous studies of gametangia of *Padina pavonica* have been virtually entirely on Mediterranean plants (Reinke, 1877, 1878; Funk, 1955; Ramon & Friedmann, 1966; Ramon, 1969*a*, *b*, *c*). In this major centre of *P. pavonica* distribution, the pattern of development in time and location seems to differ from that towards range peripheries. The higher temperature régimes and levels of illumination, leading to generally more luxuriant and perennial populations, probably entail a more continuous sequence of individual growth and degeneration, perhaps with gametangial formation, than in the north. The recent treatment of reproductive phenology in Mediterranean *P. pavonica* (Ramon & Friedmann, 1966; Ramon, 1969*c*) established that critical and extensive studies could reveal much greater frequency of gametangia than previously suspected. Gametangial material (principally monoecious [May and June] or dioecious [other months]) was detected at six locations and, at one or other location, in all months of the year on the shores of Israel. At four locations within the Bay of Naples (the classical locality for the *P. pavonica* gametophyte), large numbers of collections were made in each of July (1964), September (1963), and October (1962), slightly biasing results toward the period suggested as possibly important for gametangial detection on British shores. Collections from Split, Yugoslavia (49 gametophytes, almost entirely dioecious, out of 71 plants), reported by Ramon (1969*c*), showed similar bias since made in October (1966). In shallow depths (0–0·5 m) in the Bay of Naples, sexual thalli were comparatively rare and most of the gametophytes dioecious. This agrees well with vegetative observations and with the few old gametangial records for Great Britain. With increasing depth, the percentage of gametophytic plants generally increased and (1–1·5 m) varied from monoecious in July to predominantly dioecious in September and October. At depths of 2–2·5 m, gametophytes (all monoecious) were present in July, September and October, with the highest percentage (47·6% of sample) in September. Samples were relatively small and results may vary with larger numbers and sampling over more of the year.

Evidence from British waters, as indicated, does not permit the assignment conclusively of a significant role to wounding or frond disintegration in determining the apparently rare and late occurrence of the gametophyte here. British waters warm up more slowly, even at shallow depths, than the Mediterranean surface waters, and the equivalent (although lower) temperature conditions to the Mediterranean summer situation may not be attained until well into the September–October period, if ever, in southern England. Even in the Mediterranean (Capo Garofano, Bay of

Naples), dioecious gametophytes at 0–0·5 m in July were exceedingly rare (8·7% of sample) compared with sporophytes (91·3%) and became rarer as the season progressed (September 4·6%: 95·4%; October 0%: 100%). Since the percentage of Mediterranean gametophytes increased rapidly with depth, the limiting factor for their development in British waters may be precisely that all detected British populations grow in the shallow depths (0–0·5 m) at which gametangial development is least likely to be manifest. The November to March periodicity of Florida gametophytes of *P. vickersiae* and the slight bias towards greater numbers of *P. japonica* gametophytes in winter at Oahu may have little temperature significance for *P. pavonica*; however, since the Florida and Hawaii sea temperature régime is generally higher than the other areas considered, all gametophytes of species of *Padina* may be postulated to develop to a seasonal pattern that reflects restriction to the same narrow band of temperatures. Ramon (1969*c*) concluded that, for *P. pavonica*, there is a threshold temperature above which gametophytes appear. She correlated type of gametophyte with increasing temperature, the first formed above the threshold being predominantly typical monoecious development. In warmer waters, there is an increasing tendency for firstly male unisexual and then, at even higher temperatures, female unisexual gametophytes to form. The latter, for instance, were detected in the relatively high summer temperatures (27–30 °C) in Israeli coastal waters. Probably the situation is not quite so straightforward as this, some aspects of light levels also being involved, as they are in *P. japonica* (Allender, 1977*a*).

Tetrasporangia, by contrast, are not uncommon amongst British *Padina* specimens, particularly those collected in the inclusive period July to September; they can be detected to some extent throughout the year. Phasing of the production seems to be true for the genus wherever it appears, although times of maxima may vary. Table 1 collates all available data on distribution in space and time of vegetative and tetrasporangial plants of *P. pavonica* on the coasts of Great Britain. Interesting general tendencies are revealed. The sheer numbers of records for each county almost certainly reflect the length of historical period over which records for that area exist. Devon (most records) is by far the earliest recorded major focus; Dorset is next, and the Isle of Wight (Hampshire) is the most recent. Despite this, the three focal areas all possess large enough numbers of records to be comparable; they reveal a surprisingly consistent average level of tetrasporangial to total records for the year – 42% (Wight), 41% (Dorset), and 45% (Devon). July to September inclusive cover the vast majority of records for each focal area and therefore for the whole of British *Padina*. The odd records outside the main period show some variation with area, probably largely due to chance observation or collection, not to any difference in pattern. Note that although the total numbers of records for the three principal months show a decrease from the peak in August to the September figure, the percentage of tetrasporangial to total records shows a steady increase from July (36%), through August (39%), to September (49%). The figures for June (22%) and October (71%) neatly supplement this progression, but are based on too small a sample to be unreservedly accepted as continuing the perceived trend. The predominance of both vegetative and tetrasporangial records in the July–September period cannot be wholly a result of collecting habits; the discrepancy in numbers of records between that period and the rest of the year is too large for both tetrasporangia (65% of 80 records = 81·25% of the total) and vegetative data (157 of 188 records; 83·5%) to be accounted for solely on that basis. See below for further comment on this.

The analogous distribution of vegetative and tetrasporangial records in the north-east Atlantic outside Britain appears in Table 2. Geographically, information is less consistent than for Great Britain, but it is clear that analogous foci of distribution can be recognised (see Fig. 1 [map]). Although in southern England the Isle of Wight and Dorset foci could be considered almost continuous, they are treated separately for reasons of clarity. Northern France is similar; all records from Calvados westwards to Ille-et-Vilaine could be considered as representing a single focal area, but it is more convenient to recognise two – one to the east (the départements of Calvados and Manche), the other formed principally by the Channel Islands and Ille-et-Vilaine. The third distributional focus, further to the west, comprises Finistère and Morbihan. There are few other areas further south that are identifiable with certainty as distributional foci until the Provincia de Cadíz; the considerable information for the Basque coast and for southern Portugal tends to

Table 1 *Padina* in the British Isles: distribution in space and time*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total	Tetrasporangial %
Aberdeenshire														
Essex														
Kent								1	1				2	–
Sussex														
Hampshire & Isle of Wight					4 (4)	2	7 (3)	3 (2)	10 (2)				26 (11)	42
Dorset	1		1	1		5 (1)	15 (5)	17 (7)	21 (10)	5 (3)	2 (1)	1 (1)	69 (28)	41
Devon		1	1 (1)		1	2 (1)	17 (6)	46 (17)	18 (12)	2 (2)	1 (1)		89 (40)	45
Cornwall														
Glamorgan														
Pembrokeshire									1 (1)				1 (1)	–
Anglesey														
Lancashire														
Ayrshire														
Co. Galway														
Co. Cork					1								1	–
Total	1 (0)	1 (0)	2 (1)	1 (0)	6 (4)	9 (2)	39 (14)	67 (26)	51 (25)	7 (5)	3 (2)	1 (1)	188 (80)	
% Tetrasporangial	–	–	–	–	–	22	36	39	49	71		–	43	

* Only authenticable records specifically dated at least to month have been used; details of records are given in county lists.
( ) Figures in parentheses indicate numbers of tetrasporangial records; the overall total figure in each case includes these records. For record totals of 6 or less, no tetrasporangial percentage has been calculated, since it would be unrepresentative.

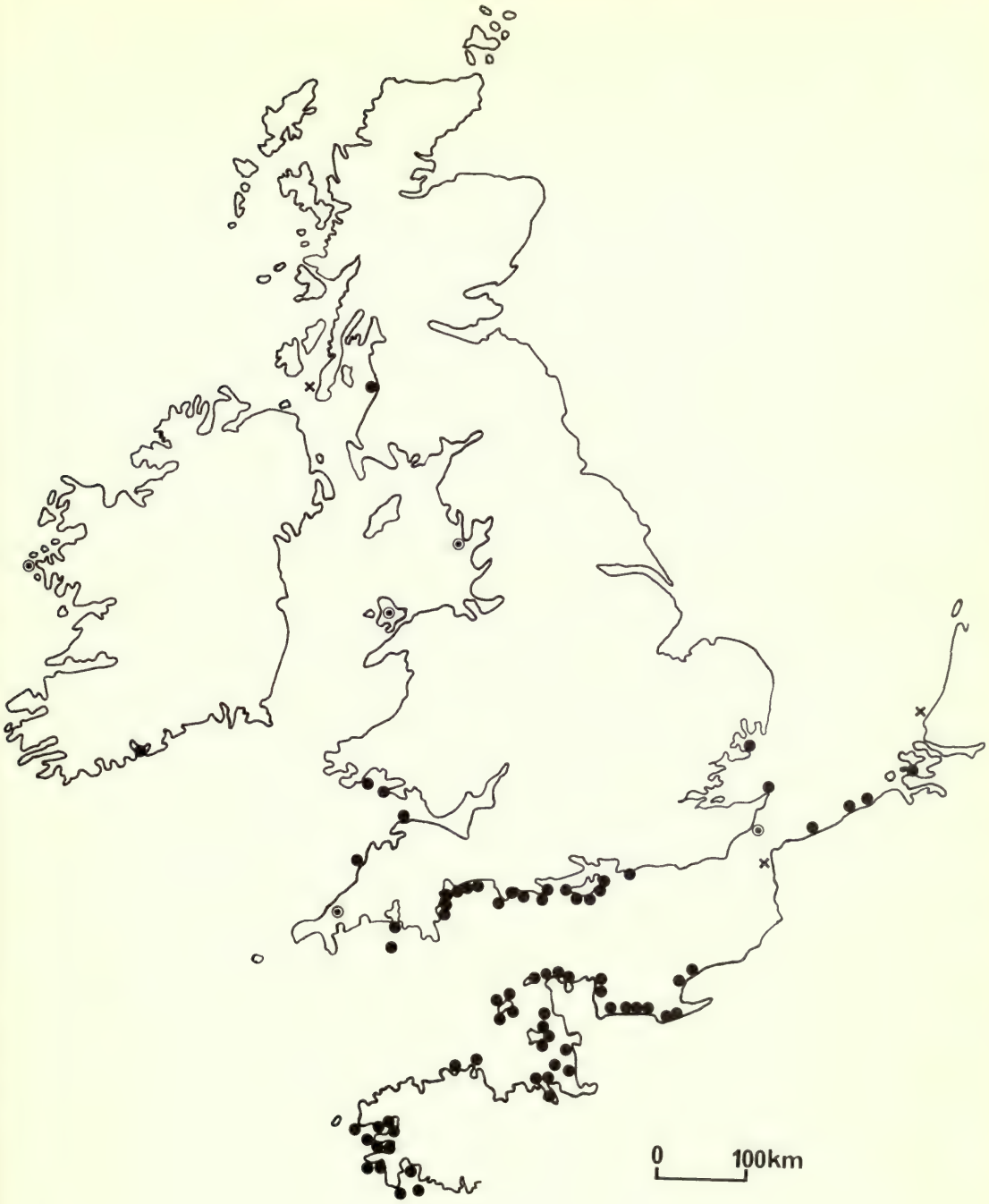


Fig. 1 The distribution of *Padina pavonica* (L.) Lamour. in northern Europe, south to Brittany.
● Authentic herbarium, literature, or MSS record.
⊙ Literature record of unknown validity.
× Drift records.
Note: The dotted circles placed in Cornwall and in Anglesey indicate imprecisely localised but important records.

Table 2 *Padina* on north-eastern Atlantic continental coasts: distribution in space and time. See notes beneath Table 1

		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total	Tetrasporangial %
Netherlands															
Belgium															
France:	Pas de Calais														
	Somme														
	Seine Maritime														
	Calvados							2 (2)	1 (1)	1 (1)				4 (4)	–
	Manche						1	2	6 (3)	9 (1)				18 (4)	22
	Channel Islands					1 (1)	2 (1)	3 (3)	5 (1)	7 (1)	1 (1)			19 (8)	42
	Ille-et-Vilaine						4	5	6	4	2			21	–
	Côtes du Nord														
	Finistère			1	1	1	4	4	2	3 (1)				16 (1)	6
	Morbihan							1	3	3				7	–
	Loire Atlantique							1	1	1				3	–
	Vendée														
	Charente Maritime														
	Gironde						1	1						2	–
	Landes														
	Basse Pyrenées							1	1	2				4	–
Spain:	Guipúzcoa														
	Santander														
	Oviedo														
	Lugo														
	La Coruña														
	Pontevedra														
Portugal:	Estremadura			2	3		1				2			8	–
	Baixo Alentejo				1			1			1			3	–
	Algarve		2						1		2			5	–
Spain:	Huelva														
	Cadíz				4 (1)	2 (1)	2 (1)	3 (1)	3 (1)	2	1		1	18 (5)	28
Total			2	3	9 (1)	4 (2)	15 (2)	24 (6)	29 (6)	32 (4)	9 (1)		1	128 (22)	
%			–	–	11	–	13	25	20	12	11		–	17	

suggest that these may be foci, but northern Spain is insufficiently studied to be certain of the Basque coast's separateness, and southern Portugal is only separated from Cadíz by the sandy and swampy Huelva. Cadíz, very near the entrance to the Mediterranean and long observed and collected, represents the start of the more or less continuous Mediterranean populations. These more southerly north-east Atlantic records demonstrate a tendency for the plant to be noticed rather earlier in the year, and in significantly larger amounts, than is the case for Great Britain. April, May, and June appear much better represented amongst *Padina* collections from Atlantic Spain and Portugal than from Britain. The predominance of both vegetative and tetrasporangial records remains, even outside Britain, in the period July–September inclusive. Largely, this is because northern French populations reveal a pattern little different from that on southern British shores. The greater abundance of April–June records from outside the British Isles affirms that the maintained July–September predominance is hardly merely a reflection of collecting habits; it could be interpreted as indicating in addition that collectors begin earlier in the year in the comparatively milder areas further south than Great Britain! There are fewer data for countries outside Great Britain on the periodicity and geographical distribution of tetrasporangia. The Channel Islands interestingly show a close correlation with the British focal areas in percentage of tetrasporangial records (42%) amongst total records; other areas (Manche, Cadíz) for which there are larger numbers of records also tend to approach similarly large percentages (22%; 28% respectively) with tetrasporangia. With further additions to the data, the similarity to southern Britain in this *Padina* characteristic may well be closer. It may reflect a parity of longevity and security of tenure amongst plants in populations above a certain (not yet identifiable and probably variable) size.

Distribution along the coasts of the British Isles

This section is organised geographically under the names of counties as accepted prior to the recent reorganisation. The order of counties is clockwise, commencing in the north-east. Within each county, locations are in a geographical order that begins at the border with or nearest to the previous county. Under each location, the arrangement of records is chronological where practicable; this best reveals both current distribution and changes that can be reliably shown to have occurred with time. Ireland, with few records, either older or recent, is treated separately and lastly. The Channel Islands, being most closely associated with the French coast, are treated as part of the continental distribution pattern of *Padina pavonica*. Standard abbreviations for herbaria are used in specimen records; where no standard abbreviation exists, one has been constructed along the same lines and is indicated by an asterisk (*) in the following list:

BEL	Ulster Museum, Belfast
BM	British Museum (Natural History)
*BMN	Bodmin Museum
BTN	Brighton Art Gallery and Museum
CGE	Botany School, University of Cambridge
CHR	Grosvenor Museum, Chester
COI	Department of Botany, University of Coimbra, Portugal
CRK	Department of Botany, University College, Cork
DBN	National Museum of Ireland, Dublin
E	Royal Botanic Gardens, Edinburgh
FKE	Folkestone Public Library, Museum and Art Gallery
GL	Department of Botany, University of Glasgow
GLAM	Glasgow Corporation Art Gallery and Museum
HAMU	Hancock Museum, Newcastle-upon-Tyne
K in BM	Royal Botanic Gardens, Kew; material now in BM
L	Rijksherbarium, Leiden, Netherlands
LINN	Linnean Society of London
LISU	Department of Botany, University of Lisbon, Portugal
LIV	City of Liverpool Museums (including LIVU – Liverpool University)
NMW	National Museum of Wales, Cardiff

NWH	Castle (City) Museum, Norwich
OXF	Department of Botany, University of Oxford
PLTH	The Marine Laboratory, Citadel Hill, Plymouth
RCR	Eastgate House Museum, Rochester
*RME	Ramsgate Public Library and Museum
SLBI	South London Botanical Institute
SRD	London Borough of Newham, Passmore Edwards Museum
STAG	University of St Andrews, Gatty Marine Laboratory
SUN	County Borough Public Library, Museum and Art Gallery, Sunderland
TCD	Trinity College, Dublin
UCNW	Department of Botany, University College of North Wales, Bangor
WRN	Municipal Museum and Art Gallery, Warrington

Throughout the distribution sections, records established under the name *Padina pavonia* are treated as though they employed the correct *P. pavonica*. The conventional symbol for tetrasporangia (⊕) is used throughout the text as required.

Aberdeenshire

Aberdeen:

C. Bauhin, 1620 : 155, Cap. 8, no. 7. '*Fucus maritimus Gallopavonis pennas referens*. . . . a D. Cargillo ex Scotia accepimus'.

Secondary records based on this are:

1. By the same name:
   How, 1650 : 43. Ray, 1670 : 120. C. Bauhin, 1671 : 155, Cap 8, no. 7. Ray, 1677 : 115. Ray, 1686 : 75.
2. As *Ulva pavonia*:
   Lightfoot, 1777 : 966. Houttuyn, 1783 : 317–318. J. E. Smith in Smith & Sowerby, 1790–1814: t. 1276 text (1/2/1804).
3. As *Zonaria pavonia*: Hooker, 1821 : 90.
4. As *Padina pavonia*: Greville, 1830 : 62–63. Harvey in Hooker, 1833 : 281. Harvey, 1846–7: t. 91 (April, 1847). Landsborough, 1849 : 129; 1851 : 138; 1857 : 138.

On p. 154 of his *Prodromos*, Bauhin adds, regarding his first two entries under Caput VIII, '. . . quorum duos priores anno 1603. D. Cargillo, Abredonia ex Scotia una cum descriptione transmisit . . .'. This is apparently the sole basis for the statements by later authors that *P. pavonica* occurred near Aberdeen, or in Scotland. Whilst Bauhin's remarks imply that Cargill sent material from Aberdeen, they cannot be taken as firm evidence that the specimens were collected in that neighbourhood; they may have come from anywhere. The legend of the actual *growth* of *P. pavonica* in Scotland seems to date from How (1650), who indicated no basis additional to Bauhin for his statement: '. . . scopulis adnascitur Scotia'. This therefore seems to be an unwarranted extrapolation from the general habitat and descriptive statement in Bauhin (1620). Ray (1670, 1677), Harvey and Landsborough all expressed doubts about the authenticity of the record, although Ray later (1686) obscured his earlier doubts by repeating the habitat statement from How (1650). He evidently changed his opinion yet again, because (Ray, 1690, 1696) he subsequently dropped all reference to Scotland. As the next most northerly record on the east coast of Great Britain is from Essex, these authors' doubts were justified. Indeed, in 1846, Johnson (in Smith, Sowerby & Johnson) was already doubting that Greville had seen *Padina* in a recent state, since it was '. . . a native only of the southern shores of England . . .'. Despite the acceptance by Roy (1887 : 149) of the probable presence of *Padina* in Scotland pre-1603, we cannot concede that there is adequate evidence of the species ever having grown on eastern Scottish shores.

Plate 1 **A:** Sloane Herbarium, H.S. 114, f. 26, no. 2 [BM]. The Buddle specimen labelling is self-explanatory. **B:** Dale (1730: Tab. II, facing p. 18). Harwich. The '. . . Stones that lie before the Cliff . . .' can be clearly seen at I in the lower right-hand corner.

A

2. Fucus auricularis Regalpini C.B. 368

Fucus maximus Galli pavonij
primus Lobelius C.B. pin. 155

Fucus cut Mor. Phil 3. Tab 8. f. 15

Fucus pavonius. 28. 1631. Ulva pavonia. Syst. Nat. vol. 3. p. 719.
Sp. Pl.
R. Hist. 75. Eb. 43. 14.
a me collect. prope
Harwich

B

A. *The greater* Light-House B. *The leſſer* Light-House C. *Harlow* Ferry-House D. *The River Stour which divides* Eſſex *and* Suffolk. E. *The* Orwel *a back comes from* Ipswich. F. *The* Haven. G. *The* Cliff. *when the* Beacon *ſtood*. H. *Boys gathering* Copper-Stones. I. Cliff Stones. K. Arwarton *in* Suffolk.

R. Sheppard Sculp.

Essex

Harwich:

Sloane Herbarium, vol. 114, folio 26, no. 2. Specimen annotated (*manu* Buddle): '*Fungus auricularis Caesalpini* C.B. . . . *Fucus maritimus Gallopavonis pennas referens* C.B. . . . a me collect. prope Harwich . . .'; additionally annotated at different times with other names [Plate 1A].

Dale, 1730 : 345, no. 8; 1732 : 345, no. 8. '*Fucus maritimus Gallo-pavonis pennas referens C.B.* . . . This grows plentifully upon the Stones that lie before the Cliff, but so far down as not to be seen but when the Tide is lowest . . .'.

Secondary records based on one or both of these are:

1. By the same name:
   Dillenius in Dillenius & Ray, 1724 : 43.14. Ellis, 1755 : 88–89; 1756 : 103. Lindsey, 1851 : 124–125.
2. As *Fucus fronde sessili reniformis decussatim striata*:
   Hill, 1760 : 608.
3. As *Fucus pavonicus*:
   Hudson, 1762 : 472. Martyn, 1763 : 47.
4. As *Ulva pavonia*:
   Camden & Gough, 1789, vol. II : 70.
5. As *Padina pavonia*:
   Batters, 1894 : 14; 1902 : 54. Milligan, 1965 : 322.

Volume 114 of the Sloane Herbarium is volume I of *Herbarium Vivum Plantarum Britannicarum à Dno. Adamo Buddle confectum* (Dandy, 1958 : 102–108). It is possible that the specimen of *Padina pavonica* from Harwich (Plate 1A) in this volume was collected from the drift, although plants of this species usually disintegrate *in situ*; the specimen is in a good state of preservation and could not have been floating for long. In any case, Dale's record is strong evidence that the Buddle specimen was not drift. The work by Taylor & Dale fortunately includes a plate (Tab. II, facing p. 18; reproduced here as Plate 1B) that shows the position of the Cliff and Cliff Stones, just south of the town of Harwich as it then was. This probably corresponds to the position of the shore rocks still present below the Tower Hill lighthouse in the modern Harwich Harbour.

Kent

Margate:

Rev. G. R. Leathes (HAMU); also MS note by D. Turner.
S.W.W. in Herb. J. McNab (1810–1878) (DBN).
No. A415, no other data (UCNW).
Smith, Sowerby & Johnson (1846 : 47), frequent on south coast, in calm rock pools exposed at low water, '. . . at Margate, Dover, and other places along the shores of Kent and Sussex . . .'.

Foreness Point:

Wood (1868 : 14–15; 1874 : 12), large colony on Long Nose Spit [see text of this county entry].

Isle of Thanet:

VIII. 1871; 19.IX.1883, Gisby Coll. (RME).

Dover:

Smith, Sowerby & Johnson (1846 : 47) [see Margate, above].
Secondary records probably totally based on the above are:
Batters (1902 : 54) and Holmes (1908 : 75), both reporting Margate and Dover; Lyle & Ridley (1925 : xxi), reporting South East Kent.

Only in the case of Sussex has it been possible to locate previous specimens or literature on which the statement by Smith, Sowerby & Johnson may have been based; the records clearly are Johnson's, but whether they depend on his own observations, verbal information from others, or

data from untraced specimens, is not known. Johnson may have seen an annotation in a copy (Cryptogamic Library, BMNH) of Turner & Dillwyn's (1805) *Botanists' Guide* . . . This interleaved copy was Turner's working text; it bears (opposite p. 362) the annotation [MS D. Turner]: '–[*Ulva*] *pavonia*. On rocks at Margate, abundant. *Rev. G. R. Leathes*'. This entry is not dated, but Leathes collected in Margate in 1808 [*Ulva echinata* Roth; specimen in Smithian Herbarium, LINN], well within Dawson Turner's periods of maximum activity and when he is likely to have made such notes. It is strange, in view of 1808 being during the run of *English Botany*, edition 1, and of the fact that Turner, Smith, Sowerby, and Leathes were all well known to each other, that the record was not published there. Leathes probably collected specimens at the time; Hancock Museum, Newcastle, holds an undated Margate specimen clearly attributable to him. We can trace nothing about the other undated herbarium specimens from Margate listed above.

Wood (1868, 1874) made precise statements in his introduction: '. . . Some years ago . . . a large colony . . . growing upon a ridge of rocks running seaward from Foreness Point, at Margate [i.e. Long Nose Spit] . . . it was the *Padina pavonia* itself – just the very last species I would have expected to find at Margate, . . . to find an alga which is mostly confined to the extreme south, off the Margate shore, which lies open to the north wind and gets full benefit of it, was a circumstance which could hardly be expected . . .'. No material collected by or connected with Wood has been located, but there are contemporary specimens of uncertain provenance in the Gisby Collection (Ramsgate Museum) which may have been collected in Thanet in 1871 and 1883. J. T. Neeve was aware (1891, only 23 years after) of Wood's remarks about *Padina* in Kent, because he stated in his *Field Notes* (Introduction) that he went '. . . to investigate the Foreness Point where I have read that the beautiful *Padina pavonia* has been found many years ago by Rev. M. Wood the naturalist . . .'; he never reported finding material. We (J. H. P.; I. T.) have made a very careful search over the area during the Kent Coast Survey period of more than ten years, but have never seen growing there, nor in the drift, even a single specimen of *P. pavonica* (Price & Tittley, 1972). It seems, therefore, that the first record from Kent must be regarded as dating from just later than 1805 (? 1808), and the latest as from before 1868, since Wood (*loc. cit.*) then wrote of '. . . Some years ago . . .'. Unless further supporting evidence is forthcoming, the later Gisby records are open to too much doubt to be admitted.

Sussex

Bognor:

Hill (1760 : 608), '. . . On Bognor Rocks, 1750 . . .' [as *Fucus fronde sessili reniformis decussatim striata*].

Herb. Mrs Robinson (BM) coll. 1831.

[?] Herb. Merrifield and Ormerod (BTN) (provenance not clear, location may be Sidmouth).

Sussex:

Smith, Sowerby & Johnson (1846), places along the Sussex shores.

Hill's manner of citation indicated that he almost certainly saw plants attached on Bognor Rocks in 1750. Access was probably reasonably easy in his time. Although the Robinson specimen could have been drift, it is in excellent condition; since it consists of several axes with sand between their intertwined prostrate systems, it could not have been long detached. In Britain, cast up material of *Padina* is now rare, either as fragments or (less commonly) as complete plants; disintegration *in situ* is more common. For continental coasts (Netherlands, Belgium, NE France) there are earlier reports of material thrown up from the drift, especially still attached to small stones. These reports are of a similar mid-19th century vintage to the Bognor Regis material and the phenomenon may have occurred more frequently then, reflecting, it may be speculated, denser populations.

This single Sussex record is from the most easterly location on the south coast of England actually represented by extant material, and modern verification would be of particular interest.

Material from Kent is available only for the north coast. Careful studies in the Bognor area in September 1969 and in August 1972 failed to reveal plants currently established there. It would have been a surprise to find plants in any part of the Bognor Regis intertidal as it now is. The Robinson material seems unlikely to have come from any depth into the infralittoral. Smith, Sowerby & Johnson's record was probably secondary, although Johnson may have included original observations.

The Bognor Rocks area has, over the last 250 years, shown considerable change in configuration, due to sand-shift and local sea-level changes associated with the slow sinking of SE England. The extent to which the Bognor Rocks break water at full tide, and their accessibility at other states of the tide, have been so much reduced that even at low springs a boat is needed for easy access. Other aspects of the physical environment may have varied, but there may simply no longer exist in this area those conditions of substratum tolerable to *Padina*.

Isle of Wight*

Bembridge:

Hambrough in Venables (1860), A. G. Moore; *Morey* (1909); Blaikley (1964); 31.v.1973, Boalch, P88/1/16, ⊕ (PLTH); 19th century (BEL).

Bembridge Lagoon:

1.x.1962, J. H. P.; 23.ix.1968, W. F. Farnham; early v–mid x.1971, mostly >3–4 cm size, ⊕, Norris (1972, unpublished).

Bembridge [Forelands], SZ 648866:

4.viii.1970, W. D. R.

Sandown:

19th century (BEL); coll. S. Bradshaw, 19th century (BM), ⊕.

Shanklin†:

v.1874, Herb. Fox Wilson; Grattann (1873–4), abundant in rock pools at Shanklin; 13.ix.1881, Emma Irving, Herb. Traill (E); July 1890, young, Herb. J. Groves (BM); 20.v.1896, Herb. George, ⊕; ix.1896, Herb. Holmes; Grattann (1896), rock pools, magnificent form, profuse in summer; *Morey* (1909), Millidge; Jackson (1926), Hearn *et al.*, rocks and pools, 3.vi.1925; ix.1925, Herb. J. Groves (BM); F. W. Smith in Herb. Batters; W. H. Grattann in Herb. Batters; Walter collection (RCR); 19th century (BEL).

Shanklin [Horse Ledge]:

Delf, *MS Field observations 1922–33* (BM): ['*Haliseris*' (= *Dictyopteris*) pools on Horse Ledge]:

22–28.iv.1922, *Padina* absent; 24–26.v.1922, small quantities in rock pools, MTL–LW, ⊕; 15.iii.1924, (Delf, Ritson & Grubb), *Padina* absent as yet; 3–5.vii.1925, three bits of *P. pavonia*; later in vii.1925, in areas around fringe of pool, especially SW and NE corners; vii.1925, plentiful all over shallow upper ledge pools, ⊕; 25–26.vi.1926, (Ritson), sparse *P. pavonia*, overgrown by ? *Asperococcus* in main pool; 11–13.iv.1933, absent as yet.

Shanklin [Horse Ledge], SZ 587802:

29.vii.1969, 4.viii.1970, W. D. R., W. F. Farnham.

[Shanklin]†, Luccombe Ledge:

Hambrough in Venables (1860, ? 1867), sandy rocks; *Morey* (1909).

* From this point onward, secondary records are sufficiently uncomplicated to be indicated in *italics* following the primary record on which they depend.

† Records probably derive from Horse Ledge; for details, see text.

Luccombe:
Foslie (1893)‡; *Morey* (1909)‡.

Ventnor:
Telford Jones, A1726, in Herb. Currie (UCNW).

Steephill:
vii.1883, Telford Jones, A1727/8, in Herb. Currie (UCNW); *Foslie* (1893)‡; *Morey* (1909)‡.

St Lawrence:
ix.1836, Herb. G. W. T. H. Fleming, two specimens, ⊕ (BM).

Brook[e] Bay:
viii.1911, no other data (LIV and LIVU).

Near Brook:
ix.1920, 'drifted', Herb. J. Groves (BM).

Compton Bay:
ix.1929, Herb. J. Groves (BM).

Colwell Bay [Warden Point], SZ 324878:
30.vii.1972, W. D. R.

Colwell Bay:
1922, Herb. J. Groves (BM); undated, Herb. J. Groves (BM).

Isle of Wight general [often as Hampshire (Isle of Wight)]:
ix.1860, coll. Miss Burnett (BM) [Plate 3B, upper specimen]; Holmes (1900, 1920); Batters (1902); vii.1949, [A.] Bursa & [F. R.], Irvine (E); Herb. Robertson (GLAM).

The Isle of Wight is the furthest east of the three major long-established south coast foci. Norris (1972, unpublished) suggested that his specimens from Bembridge lagoon, growing near a large sewer outfall, may have been adapted to and stimulated by the effluent; plants grew much more quickly overall than Lyme Regis specimens from clear water, even when both populations were grown in culture medium with 0·5% effluent content. This stimulation may partly account for the present luxuriance, but is not likely to have been effective for long enough to have been involved in the establishment of early populations. Bembridge area records (unfortunately not always more accurately localised) exist from 1860 to the present, with emphasis on the last 15 years. That emphasis has probably resulted from more workers, rather than from more *Padina*. The recent records have involved two distinct Bembridge areas. The lagoon area, described by Norris, carries a relatively luxuriant population of *Padina* which still covers only about a quarter of the area of the large pool retained at low water by the seaward rock ridges (Long Ledge, see later). This area of the pool, unlike the remaining rocky areas, has as its bottom yellow clay (Bembridge Beds). A small part of this, approximately 18 × 9 m, was covered in 1971 by *P. pavonica*, but only on the slightly raised ridges of more solid mudstone, in depths of about 0–0·4 m at normal low waters of spring tides. Earlier (1962) observations by one of us (J. H. P.) tally with this, although *P. pavonica* probably then covered a rather smaller area there. Bembridge Forelands area includes Long Ledge, a series of rocky ridges, lying some 25 m offshore at high water level. The long Ledge runs almost parallel to the shoreline, dipping gently to shoreward and toward the north-east; it is

‡ Based on a small text by Parkinson, C., *c.* 1890, *The Marine Algae* (*Seaweeds*) *of the Isle of Wight*. Parkinson apparently lived in Ventnor, where the work was published. Foslie, Batters, Morey, and Holmes had certainly seen a copy of the text. Despite prolonged search, we have been unable to locate the work.

only gradually exposed by the ebbing tide. Extensive *Padina* was found (1970) growing on the slopes of the ledge where the rock was covered by compacted sand and silt. Plants were also present in shallow rock pools, giving a total vertical amplitude of about midlittoral down to below MLWS.

The earlier records from Brook[e] Bay (1911, 1920, drift), Compton Bay (1929), and Colwell Bay (1922), with the recent (1972) rediscovery by W. D. R. of a population in Colwell Bay (near Totland, on the west coast) considerably extended the known Isle of Wight distribution. Off Warden Point, a platform slopes gently towards the north-east; a second, smaller, platform clears on the north-east side of Colwell Bay. Soft, almost muddy, sediments covered the surface of these rocky platforms and both supported populations of *Padina*.

Although the precise location is not always known and it does not have the earliest *Padina* record, Shanklin is the area with the most consistent history of records for the Isle of Wight. Horse Ledge [also known as Shanklin Ledge (Delf) and (probably) Luccombe Ledge (Hambrough in Venables)] is likely to have been the actual location in all cases. Elsewhere, the beach in front of the town is of sand at the base of 45 m cliffs, and is divided by low wooden groynes to restrict erosion and sand-transport. South of the pier, there is a scattered shingle of overlying white pebbles. Neither of these circumstances is likely to encourage *Padina* growth, although it remains possible that local and ephemeral substrate changes have eradicated populations other than on Horse Ledge. The Ledge actually consists of a number of gently southward-sloping shelves of rock trending seaward at right angles to the shore. *Padina* has been identifiably established there for some considerable time, even omitting those unsupported records for which there is no more precise location than 'Shanklin'. Hambrough's data appeared in 1860 and 1867; Grattann's in 1873–4 and 1896; and there are approximately contemporary supporting specimens in some herbaria. Delf's first records date from May 1922, and the discovery by Miss Hearn and others on the Isle of Wight Natural History Society trip (3.vi.1925) '. . . among the rocks and pools . . .' can only have referred to the Ledge. Subsequently, *Padina* was observed there in variable amounts during 1925, 1926, September 1968, July 1969, and August 1970. The more recent observations revealed *Padina* in small patches in scanty sediment on the wet rock surface, in shallow pools, and on those parts of each shelf that remained in shallow depths below low tide level. If the imprecise Shanklin records are admitted as referring to the same population, *Padina* seems likely to have been present on Horse Ledge continuously for at least 100 years, and very probably much longer.

Dorset

Studland:
23.iii.1890, K. Holmes (NMW).

Swanage:
Pulteney (1799); *Pulteney* [& *Rackett*] (1813); *Pulteney in Greville* (1830); M. E. Gray collection, viii.1859 (CGE), ix.1859 (CGE), vii.1861 (SLBI), vii.1861 (BM), 1861 (BM); Herb. Batters, 23.vi.1885, 1890 E. George, 24.ix.1891, ix.1897 E. George; 1.x.1890, K. Holmes in Herb. Holmes; Batters (1902); Herb. Robertson (GLAM).

Chapman's Pool:
ix.1894, Batters BMSC 9538; Batters (1902); Carter (1927), viii.1924 and summer 1925; 2.x.1960, J. F. M. Cannon, no. 2882, muddy rocks at HW; Burrows (1964), mid-littoral; 23.x.1964, ⊕, E. M. Burrows; x.1965 (Herb. Russell); Holmes MSS [*Victoria County History, Dorset*, unpublished].

Chapman's Pool, JY 957770:
25.ix.1972, W. D. R.

Kimmeridge:
x.1965 (Herb. Russell).

Kimmeridge Bay, SY 907719:
12.viii.1969, 6.viii.1970, 22.iv.1971, all W. D. R.; 14.vi.1972, 9.ix.1972, to date, E. M. Burrows, '. . . The species has spread considerably in Dorset over the last few years . . .', 6⊕ specimens, P88/1/14 (3), P88/1/15 (3) (PLTH).

God Cliff, 200 m east of Wagon Rock, [Brandy Bay]:
1.viii.1976, John Henthorne.

Lulworth Cove:
Pulteney (1799); *Pulteney* [& *Rackett*] (1813); *Pulteney in Greville* (1830); Batters (1902); Carter (1927), viii.1924 and summer 1925.

Lulworth Cove, SY 824798:
31.vii.1967, Burrows & Da Silva, flat pools at top of shore.

Lulworth Cove, SY 826798:
vii.1972, E. M. Burrows.

Lulworth:
Holmes MSS [*Victoria County History, Dorset*, unpublished].

Osmington Mills, SY 734817:
vi.1921, R. D'O. Good (STAG); 12.vii.1972, E. M. Burrows; Richardson, no. 3333, ⊕, W. D. R., 9.ix.1976, occasional groups.

Bowleaze Cove, in and near:
E. M. Burrows, no other data.

Weymouth [dated records]:
1797, volume named [and ? collected] by Stackhouse, p. 10, six specimens, one with fine basal stoloniferous ramifications (BM); Pulteney (1799); *Pulteney* [& *Rackett*] (1813); *Pulteney in Greville* (1830); Herb. L. W. Dillwyn (K in BM); 1849 (WRN); 16.vii.1850, Mrs M. E. Gray (CGE); 1857, coll. Miss Burnett (BM) [Plate 3B, lower specimen]; Damon (1860); vii.1864, Leipner in Rabenhorst, *Algen Europas*, no. 1753, shallow rocks in shallow pools at half-tide; vii. 1881, K. A.[ppleford] in Herb. Holmes (NMW); viii.1882, Herb. Holmes; Holmes (1882); 1882, coll. T. H. Buffham; viii.1883, ⊕; vii.1885, R. V. Tellam in Herb. Neeve (FKE); viii.1885, Buffham in BMSC 9541; vii.1888, Buffham in BMSC 263, 264, 265, 9542; 19.ix.1891, E. George; ix.1892, Batters, ⊕, P88/1/3 (PLTH); ix.1892, Batters in Herb. Neeve (FKE); ix.1892, Herb. Batters; ix.1892, Batters in BMSC 9535, 9536, 9537; viii.1893, Herb. Batters; viii.1900, Herb. J. T. Neeve (BM); Batters (1902); Williams (1905), summers 1904, 1905; Sedgwick (1922), common.

Weymouth [undated records]:
Herb. Moseley; Herb. E. M. Holmes (NMW; BEL); Holmes MSS [*Victoria County History, Dorset*, unpublished]; Herb. Neeve; Herb. Robertson (GLAM); Herb. Brodie, (MS D. Turner) (GL); Herb. Brodie, Mr Woods (GL).

Weymouth, The Look Out:
Withering (1796), Withering & Withering (1801, 1812, 1818, 1830), '. . . Mr. Stackhouse . . . rocks at low water mark . . .'; (1799 ?), '*Ulva pavonia* near ye Look-out-Weymouth', plants with stolons [for further data, see Dawlish entry for details of E. P. collection book] (BM); Smith & Sowerby (1.ii.1804), tab. 1276, *Ulva pavonia*, '. . . Gathered by Mr. Bryer and Mr. Pilkington . . .'; original drawing for illustration to *English Botany*, tab. 1276, near the Lookout, Mr S. P. Bryer, Wm Pilkington, and others (BM); A. B. Lambert in Herb. Hooker (K in BM); nos A415, A416 (UCNW); 6.viii.1970, W. D. R.

Weymouth, Nothe Pools:

Gosse (1854, 1856), end v to autumn; 20.viii.1906, 15.vi.1908, 13.ix.1909, 6.xii.1911, all coll. A. D. Cotton (K in BM); 13.ix.1909, A. D. Cotton (NMW); 23.xi.1908, A. D. Cotton, (BM), ⊕.

A. D. Cotton, *MS Field Notes* (BM):

13–22.vi.1908, small *Padina*; 21–27.xi.1908, Nothe pools and below, very abundant; 22.i.1909, Nothe pools and rocks, old plants; 13.ix.1909, Nothe pools, some in pools and shallow water below stone groynes, very abundant; 17.xi.1909, Nothe pools rather bare, apparently no *Padina*; 11.iv.1910, Nothe pools, *Padina* apparently absent; 6.xii.1911, Nothe pools, *Padina* apparently absent.

Weymouth, Nothe Rocks:

Carter (1927),viii.1924 and summer 1925, fairly abundant, flourishing in sandy rock pools on stiff Oxford Clay, revealed only at low water of spring tides.

Sandsfoot Bay, near Weymouth:

c. 1850, Merrifield in Miss Barnard collection (NWH).

Under Sandsfoot Castle:

Gosse (1854, 1856); 31.vii.1967, 5–10 plants on protected ledge, MTL, in probable pool at lower tide states, Burrows and Da Silva; same location, undated but subsequent, W. F. Farnham.

Ledges between Sandsfoot Castle and Byng Cliff:

Gosse (1854, 1856).

Portland Bay:

24.ix.1893, E. George.

East Fleet, SY 650773:

31.vii.1977, W. D. R. Narrow area with strong tidal currents; few scattered colonies in shallow (0·2 m below LW) water, on silted bottom or boulders, ⊕.

Lyme Regis

24.vii.1802, Lyme, E. P., '. . . Growing in immense quantity in shallow pools – when magd. the seed appear distinctly as black grains, in the two lower semi-circles – their color when fresh of a dirty white far less beautiful than those of Dawlish' [see Dawlish entry for details of E. P. collection book]; Plues (1864), no date, rock pools; Walker (1884), rock pools; 29.viii.1971, in large and small pools, ⊕, Norris (1972, unpublished); 17.ix.1971, W. F. Farnham, shallow pools on ledges; not dated, W. F. Farnham, shallow pools on ledges, sterile specimens (PLTH).

Lyme Regis, SY 333914:

29.vii.1972, W. D. R.; 9.ix.1976, ⊕, W. D. R.

Dorset general:

Harvey (1833); Anon. [Tregelles & Parke] (1952).

The comparatively rich heritage of Dorset data for *Padina pavonica* suffers geographical imprecision, especially in records from before the mid-19th century. 'Weymouth', 'Swanage', and 'Lyme Regis' can often only be elucidated by making the assumption that current or recent locations of populations have altered little in many years. Often enough, this is a reasonable assumption; equally often, there is little foundation for it. Local substrate, configuration and wave-action changes, artificially or naturally induced, have affected certain localities associated with towns (e.g. Swanage; Weymouth) the importance of which has grown in the last century; precise siting of older records by comparison with modern populations is in those areas not possible.

Studland is the most easterly reported locality, although there seems to be no valid reason why plants do not appear in areas of Poole Harbour. In Studland Bay, north of Handfast Point and near the village of Studland (SY 042824), there is a small area of rocks forming the kind of habitat commonly exploited by *Padina pavonica*; no specimens were detected there on 5 August 1970, or at various dates in summers 1975 and 1976, but since 'Studland' is not qualified on the Holmes specimen, the same area may not have been involved.

One of the major Dorset localities for *Padina* is the Swanage area. Numerous records, well distributed in time, exist since Pulteney (1799) recorded the plant from there; some, for example that in Greville (1830), are undoubtedly secondary. Batters's (1902) record was probably partly based on previous data, although collections by Batters himself and by George were available to him by then. Although it is possible, the years recorded on specimens (1859, 1861, 1867, 1885, 1890, 1891) doubtfully represent really discontinuous appearance of the alga at Swanage. There is no way of knowing whether Holmes, his wife, Batters, and others who consistently visited Swanage on collecting trips during the second half of the 19th century, equally consistently observed *Padina* on all those trips. It seems likely that once they accepted the common appearance of a particular alga, especially one so obvious as *P. pavonica*, they would in future be inclined rather to note its sudden and discontinuous absence than its customary presence. Nevertheless, recent careful searches (May 1964, 5 August 1970, April 1974, May 1974, frequently in 1975 and 1976) of the intertidal rocks between Swanage Pier and Peveril Point and of the rocks off Peveril Point itself failed to detect any plants of *P. pavonica*. Cotton (1908–11) and Grubb (1936), both of whom studied Peveril Point in detail, similarly did not record the alga. If a population were present up to the early years of this century, it has since, for whatever reason, died out and never apparently re-established in the immediate area. In critical cases like this, the availability of information concerning *exact* locations visited by 19th century workers is vital; the imprecise locational data are all the more regrettable.

Chapman's Pool has a fairly long history of the occurrence of *Padina pavonica*, but based on fewer records than for Swanage. Some of the older 'Swanage' data may really be referable to this spot. The earliest traced record is unequivocal since luckily represented by material; from that time (September 1894) until now, recording has been fairly consistent. The gaps in recording (between Holmes and Batters, in the early 20th century, and 1924–25; between 1924–25 and 1960) probably have no other significance than chance absence of publication or specimen preservation. Thereafter, the population was consistent and is still extant. A series of step-like cementstone ledges, tilted slightly towards the shore and covered by a slimy, almost muddy coating of eroded shale, offers a suitable habitat for *Padina* and was certainly the source of all recent collections; on 25 September 1972, among quite large local patches of *Padina* were some notably large individual plants.

Kimmeridge (in the Bay, below Gaulter Gap) seems not to have been recorded as a location for attached *Padina* until 1965. Cementstone ledges similar to those at Chapman's Pool run out to seaward; parts of these ledges are fully exposed at low water, but the rocks between them remain submerged. In this shallow water between the ledges, *Padina* colonies were detected in the detailed surveys of 1969–71; a few other small colonies were noted in pools on the west side of the bay. Populations are present in the shaly debris covering the hard rock surfaces at both these places. Absence of Kimmeridge Bay from older published or herbarium records of *Padina* does not necessarily indicate that Burrows's comment regarding recent spread applies directly there. Like Chapman's Pool, it may have hitherto been included under the blanket name 'Swanage'.

Lulworth Cove was first mentioned by Pulteney (1799) and repeated in Greville (1830). Holmes's MS for the unpublished *Victoria County History of Dorset* also lists Lulworth, but appears to be original or at least confirmatory from observation. There seem to have been no subsequent data confirmatory of *Padina pavonica* in Lulworth area until the visits by Carter in 1924–25, and by Burrows in 1967 and 1972. A similar, although more recent, sparse history of records applies to Osmington Mills, where the probable reason is relative rarity of shore visits by collectors; that reasoning is most unlikely to be applicable in as famous an area as Lulworth. There may well be additional small populations (as in Brandy Bay, God Cliff) remaining to be

detected in suitable local conditions elsewhere along this eastern Swanage-to-Lulworth section of the Dorset coast.

Most of the records localised to the Portland Bay and Harbour area also specifically state Weymouth. Weymouth is by far the earliest and most consistently recorded location for *Padina pavonica* on the Dorset coast. Even those records (1797 and a little earlier), dated some 40 years before the earliest traced data for the Isle of Wight, are more than 120 years later than the earliest Devon coast data (see below). The oldest specimen traced, clearly from a vigorous population, is actually antedated slightly by publication (Withering, 1796) of the record from the same place (Weymouth, Lookout) and by the same collector (Stackhouse); other material, collected earlier, probably did and perhaps still does exist. Another specimen, recently (1971) acquired by BM in a mostly early 19th century volume, may have derived from the same location and perhaps even from the same collecting trip. The compiler, initials 'E. P.' [? an ancestor of Edward Parfitt, or a relative of the Pilkington referred to in *English Botany*, pl. 1276] made copious notes (see records and discussion under Devon) and exchanged specimens with many of the better known phycologists of his time, such as Stackhouse and Dawson Turner. The specimen of importance here is not dated precisely, but is unlikely to have been later than 1799; the annotation [MS E. P.] combines data from Withering (1796) and from the Stackhouse (1797) specimen quoted. The specimen shows the same vigorous basal stolon development as the Stackhouse specimen. Many early specimens or records carry data which clearly indicate that the collection or observation was inspired by the early Stackhouse locality data, if not actually part of the latter and provided by Stackhouse. Specimens involved with Smith's *English Botany*, pl. 1276; K in BM material from Herbs. Dillwyn and Lambert; and possibly Pulteney's (1799, 1813) observations, are examples, although the latter were almost certain to have been supplemented by personal observations. Subsequent information for Weymouth area is an even mixture of many literature citations with original observations from many different years and seasons. Specimens, derived from spots identified with variable precision, support or form exclusively most of the original observations; amongst locations that can be identified, the Lookout, Portland Bay, Sandsfoot Bay, and around the Castle (probably the incurve revealed at low water below Sandsfoot Castle, Portland Harbour) and, especially, the Nothe pools area, are of importance. Cotton's (1906–11) detailed series of seasonal specimens and field notes from the Nothe is particularly noteworthy. The series clearly demonstrates variation in *Padina* abundance and seasonality from year to year. Our own recent (6 August 1970, 5 May 1974) visits to Weymouth (SY 685786) and Portland resulted in detection of only a few small colonies to the south of the [Weymouth] harbour entrance, where rocky ledges run parallel to the shore (W→E, approximately). This area of rocks represents the 'Nothe Pools', and may also be that referred to as 'rocks near the Lookout', and 'Lookout'; we have been unable with certainty to establish the whereabouts of the latter. Further south, within Portland Harbour, Western Ledges (SY 679778) appeared to offer suitable conditions for *Padina*, but none was found. The rocks just to the south and west of Western Ledges, below Sandsfoot Castle and probably the source of earlier (Sandsfoot Bay, *c.* 1850) records, also require further examination. According to Gosse (1854), the populations at Sandsfoot and between there and Byng Cliff were established by Thompson, who took fronds from the Nothe area and scattered them in nearby similar situations, where they flourished. Plants could still be detected in 1967.

Lyme Regis has long been a popular resort and this probably accounts for the existence of the very early (1802) record. Given this very early record, with precise comments, it is surprising that no further data can be traced until the (probably primary) literature record of 1864 (Plues). The break between 1864 and 1884 (Walker) is equally mystifying; Lyme Regis did not lose popularity for holidays and natural history studies at that point. There is a further long break until the present era of reports (1971, 1972, 1976). All records are from shallow pools on ledges. Our visits (1968, 1972, 1974, 1975, 1976) have revealed, to the west of the famous 'Cobb' (the very old and massive stone quayside and harbour), a series of gently sloping, shaly ledges very similar to those at Forelands, Isle of Wight, and trending south-west, to seaward. The gentle slope of these ledges ensures that the wet rock surface drains only slowly and tends to accumulate sediment deposits. *Padina* was found (1972, 1976) to grow over a considerable part of the ledges from about mid-littoral downwards into shallow water, in some cases being truly if shallowly infralittoral. There

is no reason to doubt that these populations are the offspring of those earlier noted by E. P., Plues, and Walker.

Devon (South)

Sidmouth:

Herb. Greville, (E): vii, viii.1828, fs, Mrs Griffiths; vii.1828 (MS Cutler); vii.1828, Miss Cutler (only probably Sidmouth); vii.1829, Mrs Griffiths; vii.1829, Miss Cutler; 30.viii.1833, Miss Cutler; viii.1833, Miss Cutler; Greville (1830), Mrs Griffiths.

Miss Cutler coll. (TCD): 19.viii.1830; 8.ix.1831; 13.viii.1832; 14.viii.1833.

18.vi.1833, Dr Greville, Pollexfen in Herb. Batters; Herb. Harvey (BM), 5.vii.1833, 30.viii. 1833; 2.viii.1833, Herb. Cutler, ⊕, (BM); 30.viii.1833, Miss A. Ball (DBN); viii.1833, W. Thompson (BEL); 1833, Cutler in Herb. Gatty (STAG); Mogridge (1836); Areschoug (1843); 2.vii.1849, (E); 18.viii.1880, R. V. Tellam (BMN); viii.1880, Herb. Holmes; Parfitt (1889), abundant in shallow intertidal pools; viii.1891, Buffham (BM); viii.1891, Buffham, [BMSpC] 1453; Buffham (1893), ix.1891 [confusion between viii and ix.1891 in different parts of work; specimens supporting both months in BM]; 11.viii.1892, T. H. Buffham, ⊕, three fine plants, J. T. Neeve, *MS Field Notes* (FKE); *c.* 1892, Batters, ⊕, P88/1/2 (PLTH); ix.1894, Batters in BMSC 9539; viii.1895, Holmes, *Algae Britannicae Rariores Exsiccatae*, no. 12, (BM); viii.1901, Batters (BM); Batters (1902); Williams (1905), summers 1904–05; *Hamel* (1931) (Buffham); Tregelles (1932); 2.vii.1949 (E); Herb. Merrifield and Ormerod, location with '?' (BTN); viii, Herb. Holmes (NMW); Herb. Cork (CRK).

Sidmouth [Lade Foot Rocks], SY 106862:

26.viii.1968, 23.ix.1968, 7.iii.1969, 29.vi.1969, 1.viii.1969, 13.ix.1969, 22.vii.1970, 17.ix.1970, ix.1971, all W. D. R.; consistently present in all May–September visits, 1972–76, W. D. R., ⊕, in September.

Ladram Bay:

ix.1852, Cutler in Herb. Masters (K in BM); 8.ix.1892, Herb. George, ⊕ (BM); 20.v.1896, Herb. George; viii.1901, Batters collection; *Carter* (1927) (Lloyd Williams).

Ladram Bay, SY 095850:

14.viii.1969, 14.ix.1969, 11.x.1969, 21.vii.1970, 17.ix.1970, all W. D. R.; Norris (1972, unpublished), pools; ii.1973, M. D. Guiry, good growth; 30.viii.1974, W. D. R., J. H. P. & L. B. L., well developed populations; consistently present in all May–September visits, 1972–76, with ⊕ in September, W. D. R.

Budleigh Salterton:

vii.1810, Herb. Edward Forster (BM); Tregelles (1932).

Exmouth:

Newton (1680–83), '. . . in holes & hollow places where water stands betw. ye rocks going into ye sea abt. a mile fr Exmouth – Ntn. –' [MS note by Newton, in indicated period, in Ray (1670: at p. 115, BM copy)], as *Fucus maritimus Gallopavonis pennas referens* C. B.; Ray (1686), 'Ostendit nobis hanc plantam D. Stevens à se inventam propè Exoniam Devoniae urbem . . .'; and as secondary Stevens record repeats in all the following cases [to Turton & Kingston, 1829, 1830]:

Ray (1688, 1690, 1696; all as *Fucus maritimus Gallopavonis pennas referens* C. B.); Dillenius in Ray (1724; as same); Hill (1760; as *Fucus fronde sessili renifomis decussatim striata*); Hudson (1762; as *Fucus pavonicus*); Camden & Gibson (1695, 1722; as *Lichen seu muscus marinus variegatus*); Camden & Gough (1789; as *Ulva pavonia*); Polwhele (1797; as *Ulva pavonia*); Turner & Dillwyn (1805; as *Ulva pavonia*); Greville (1830); Turner & Kingston (1829 ?; 1830; as *Zonaria pavonia*).

vii.1850, W. H. Harvey, *British Algae*, vol. I (BM), prepared by Harvey for John van Voorst, illustrative collection for a copy of Harvey's *Manual* (ed. 2, 1849); ii.1855, J. Cocks, *Algarum*

Fasciculi . . ., fasc. iv, pl. 36, shallow sandy pools, half-tide, viii and ix, ? ⊕ (BM; PLTH); 11.i.1856, Miss Cutler (GL); 1857, Cocks (NWH); *Landsborough* (1857) (Mrs Gulson); Parfitt (1889), abundant in shallow intertidal pools, Exmouth Point; ix.1892, Batters, ex Eccles Library, P88/1/4, ⊕, location with '?' (PLTH); viii.1895, Holmes in Herb. Batters (BM); Holmes (CGE); Holmes, *Algae Britannicae Rariores Exciccatae*, no. 212 (K in BM; BM); Grattann (1896); Batters (1902); Tregelles (1932); Landsborough (BEL); no data, presented J. A. Longley (BM); no date, early MS in location (E); no date (PLTH).

Dawlish, Langston Point:
vii.1850 (E).

Dawlish Warren Rocks:
Anon., Anon., & L., S. E. (1869), S., R. S., Anon., & L., S. E. (1869), abundant in the Warren Rocks, rare in many places.

Dawlish:
4.vii.1799, E. P. (collector of majority of specimens), '. . . Beginning to grow up, all the others of the same growth . . .' [specimen from a volume of early nineteenth century vintage, copiously annotated and sent from or seen by well-known workers such as Stackhouse, collected 1790s to early 1800s] (BM); 25.vii.1799, E. P., one mile east of Dawlish, '. . . second state of growth; about 6 weeks old; showing its pink fringe . . .' (BM); 4.viii.1799, E. P., '. . . gather'd Aug:t. 4 from the same pool as those of July were taken being the only place where I found them at Dawlish . . .'; 7.vii.1799, E. P. (marked x), '. . . seed seen at x when mag:d. . . .' viii.1850, Herb. Gatty (STAG); 1876? Rev. J. T. Clough in Herb. Gatty (STAG); *Tregelles* (1932).

Teignmouth:
Herb. W. R. Sherrin (? fertile) (SLBI).

Shaldon:
Parfitt (1889), abundant in shallow intertidal pools; *Batters* (1902).

Torquay:
1825, Greville (E; BM); *c.* 1830–50, W. H. Harvey (NWH); Greville (1830) (Griffiths); Turton & Kingston (1829 ?; 1830); viii.1844 (BM); viii.1844, W. H. Harvey (TCD); viii.1844, W. Thompson coll. (BEL); Harvey (1847) abundant; ix.1848, Herb. Ravenel (BM); *c.* 1850, Wyatt in J. D. Salmon (NWH); Gifford (1853); ii.1855, J. Cocks, *Algarum Fasciculi* . . ., fasc. iv, p. 36, in shallow sandy pools, half-tide level, viii and ix, ? ⊕ (PLTH; BM); *Landsborough* (1857) (Griffiths); vii.1865, 29.viii.1894, Herb. George (BM); viii.1867, Herb. Dickie (BM); 1894, [Herb.] G. W. T. H. Fleming (BM); viii.1899, Herb. Neeve (FKE); viii.1899, T. H. Buffham (BM); ix.1889, Herb. Holmes (BM); Williams (1905), summers 1904, 1905; Holmes (1906b), Torquay area; Cotton (1907), Aug. 1905, 1906; 20.vii.1923, Herb. Thomas Wise (GL); Tregelles (1932), abundant; vii.1850, W. H. Harvey, *British Algae*, vol. I (BM), prepared by Harvey for John van Voorst, illustrative collection for a copy of Harvey's *Manual* (ed. 2, 1849); Herb. Lyon (BM); Miss Boning (BEL); no date or collector, A415 (UCNW).

Torquay, SX 935654:
Near Babbacombe, 'Field System' [=north side of Long Quarry Point, Torquay] (LIV).

Torre Abbey area:
Torquay, Corbyn's Head Rocks:
Very common round Corbyn's Head, Salter (1911).
Torquay, Corbyn's Head Rocks, SX 907632:
12.vii.1971; 22.ix.1971; 28.vii.1972, all W. D. R. [Plate 2].

Tor Abbey:

viii.1830, Griffiths, vol. I, *British Algae*, arranged according to Harvey's *Manual*, ed. 1, 4.xi. 1858 (LINN, now in BM), 26.viii.[18]35, J. B., Mrs Griffiths, *British Algae*, vol. I; viii.1836, A. W. Griffiths (E); 1836, (E); *c.* 1850, Fielden (CHR).

Tor Abbey Rocks:

16.viii.1833, Mrs Wyatt, Pollexfen in Herb. Batters; viii.1833, Blatch in Herb. Ralfs (LIV); Anon. (1855); Wyatt, *Algae Danmonienses*, vol. I, no. 11 (GL; E; DBN; PLTH, ⊕; BM, ⊕); no date or collector, A1201 (UCNW).

Tor Abbey Rocks and down towards Paignton:

Grattann (1873), abundant in shallow pools, summer annual, from early days of June or later, very plentiful this summer, all through July, hence vii.1872, vii.1873.

Torquay (*Livermead*):

1859, C. A. Johnson (BM).

Torquay (*Livermead Rocks*):

20.viii.1906, A. D. Cotton (K in BM and BM), some ⊕.

Torquay, Livermead Sands:

12.vii.1971, P. Tranter, LWMOST, on flat rocky shore, ⊕, P88/1/13 (PLTH).

Torbay, Preston Beach [Paignton]:

1878, 1880, 1892, Herb. G. W. Traill (E); 12.viii.1892, G. W. Traill (E).

Torbay:

Griffiths (1832); viii.1832, Mrs Griffiths, *British Algae*, vol. I (cf. Tor Abbey, above); Anon. (1854); Anon. (1861); 1878, Herb. G. W. Traill (E); 1880, E. H. Boning in Herb. G. W. Traill (E); vii.1882 (BEL); 1882, Boning in Herb. G. W. Traill (E); viii.1883, E. H. Boning in Herb. Batters (BM); vii.1884, Herb. G. W. Traill (9428) (BM); Parfitt (1889), abundant in shallow intertidal pools; viii.1892, F. W. Smith in Herb. Batters (BM); Batters (1902); Herb. Berkeley, n/d (GL); Mrs Griffiths, Herb. Dickie (BM).

Paignton:

1874, E. R. E. in Herb. Gatty (STAG); vii.1889, Buffham in BMSC 9540; reference coll., n/d (PLTH), rock at low-water.

Shoalstone Rocks, Brixham, SX 934567:

Richardson, no. 3326, ⊕, 6.ix.1975, W. D. R., few plants in silty pool.

Shoalstone, near Brixham:

25.x.1953, E. Clay, P88/1/8, cluster of ⊕ plants; similar specimens (juvenile; smaller), P88/1/5,6,7, (PLTH).

Plymouth:

Holmes (1906*b*); *Tregelles* (1932); '. . . Dredged in Plymouth near Duke rock', reference coll., no date [prob. about end 19th century] (PLTH).

Honiton area:

Holmes (1906*b*) [location name relates to stretch of coastline in east of county, under Holmes area system].

Devon general:

Robson (1777), secondary from Stephens source; Harvey (1833); *c.* 1851, Bratton Fleming, P88/1/9, cluster of ⊕ plants (PLTH); P88/1/10, ⊕ (PLTH); 1855, J. Cocks, *Algarum Fasciculi*, ⊕, P88/1/1 (PLTH); Anon. [Tregelles & Parke] (1952); Greville (GL); no data (CRK).

Devon has by far the earliest records of British *Padina*. The species was well established during the late 17th century; although locations have probably varied in density of populations at different times, there has been no subsequent indication of total loss of the alga. It is unfortunate that no contemporary localised algal material clearly identifiable with Ray's *Historia plantarum*, vol. I, 1686, has ever been traced. Buddle's collection (BM) contains much from Rev. L. Stevens ['Stephens'; collected mostly in Devon and Cornwall], but of *Padina* there is only the Harwich specimen (see Essex). Even so, the detailed and obviously original MS observation by Newton, from the same or similar location and period, indicates that there is no reason to doubt the authenticity of the [Stevens's] observation at Exmouth. Ray (1688) used the English form 'Exmouth', as in all his subsequent Latin or English treatments; his earlier (1686) use of '. . . propè Exoniam Devoniae urbem . . .' was therefore either an error or an adaptation of the Latin geographical name most nearly fitting his needs. Stearn (1966 : 220) indicated that *Exonia* is the Latin name for Exeter, not Exmouth.

For many years, this original Stevens record provided the only basis for the inclusion of *Padina pavonica* in floristic works on the British Isles. Even after the species had been detected elsewhere, or thought to be so, the record was still quoted; many examples are provided in the records list. Because of its historical importance, the original Stevens record is considered here out of geographical order. Subsequent recording from this geographical area has been patchy and some doubtless secondary. Most later records, however, are supported by original comments based on specimens; they are fairly evenly spaced throughout the 19th century, ending with that of Tregelles (1932). It is not clear whether or not Tregelles based the observation partly on his own experience, because the list of locations is generally qualified as being from 'various observers'. Numerous visits since 1969 have failed to establish the authenticity of this recent record from Exmouth. To the east of the mouth of the Exe (SY 025794), the rocky area (Conger Rocks, Maer Rocks, Orcombe Rocks) was densely covered by *Enteromorpha*, leaving little clear space in which *Padina* could have been growing.

Exmouth and Dawlish, to the west on the opposite bank of the Exe, tend to be associated. Older records were sometimes actually localised to an area between Exmouth and Dawlish. Most of that shore-line is sandy or estuarine but near Dawlish Warren, rocks similar to those at Sidmouth break water off Langstone Cliff (SY 980780). Despite a careful search, no *Padina* was found there, although there are 1869 statements that the alga was '. . . growing abundantly . . .' on Dawlish Warren rocks; specimens dated in 1850 and 1876 lend support to this, some being actually localised to 'Langston Point'. The earliest records localised to Dawlish are of great interest, as they represent a genuine earlier attempt to assemble seasonal data like those in Cotton's 1906–11 *Field Notes* and specimens from Weymouth. E. P., in the volume now held in BM (see Dorset and Devon record lists), collected *P. pavonica* consistently, from the one pool where he could find plants, over the period 4 July to 7 August 1799. From being just a recognisable population on 4 July *Padina* had attained tetrasporangial production by 7 August. The location can be pin-pointed exactly, since one specimen is annotated 'one mile East of Dawlish', coinciding with the rocks below Langstone Cliff. A population was therefore present at least from 1799 (and probably earlier) until 1876 (and probably later), although it seems currently to be absent. South of Dawlish, rocky areas similar to that at Langstone Cliff, possibly bearing *Padina*, exist at Cowhole Rock (SX 962762), Old Maid Rock (SX 963761) and Horse Rocks (SX 961757).

Large numbers of records from Sidmouth, the most easterly locality in Devon, exist for the period 1829–33 [–1843]; most are based on herbarium material. Many collectors, including Miss A. Ball, Miss Cutler, Greville, Mrs Griffiths, and W. H. Harvey, contributed. Thirty-seven years absence of recorded information after 1843 culminated in the long series of records from 1880 to date; with few exceptions, these later records are merely localised to Sidmouth. In the early years from 1880 onwards, collectors most involved included Batters, Buffham, Holmes and Tellam. The Tregelles record of 1932, the first for 27 years and not added to until 1949, is almost certain principally to be secondary, although the subsequent (1949) record derives from material. Some of the older records may have been collected from Chit Rocks, west of Sidmouth near Jacob's Ladder. *Padina* now seems not to grow on these rocks, but there exist scattered populations in pools and on gentle slopes of the soft slimy rocks surfaces, somewhat further west on Lade Foot Rocks, below

High Peak. Observed seasonally since 1968, the species is locally widespread there, although never prolific.

West of Sidmouth, on similar rocks (Sandy Cove–Herm Rock–Ladram Rock–Smallstones Point area), colonies of *Padina* occur around Ladram Bay. These are of some longevity, perhaps discontinuous as to individual population, with almost all the evidence in the form of specimens; the earliest is September 1852. Detailed recent winter and summer observations, from 1969, have demonstrated perennation in the form of well-grown, if somewhat ragged, plants, without even *nearly* complete die-back.

Budleigh Salterton (SY 080820) is represented by only one early (1810) collection; Tregelles (1932) is undoubtedly secondary. The area seems initially an unlikely source of *Padina*; the present shore is of smooth, light-grey shingle, grading in the west into sand below high cliffs. East of the town is the marshy valley of the River Otter. A rocky area (Otterton Ledge – Danger Point – Black Head) east of the river is similar in appearance to rocks at Sidmouth and Ladram Bay; the area is difficult of access and has only recently been searched. Access probably always was difficult and raises some doubts as to the validity of the early record. Edward Forster customarily removed earlier script from his specimens, re-writing the labels (Dixon, 1959); it is not known how accurately data were transcribed. Potential loss of information in transcription and possible original loose application of the place name leaves some doubt. Luckily the record is not critical; there are adjacent populations to east and west.

The single Teignmouth specimen could have come from Sprey Point rocks, north of the Teign Estuary; we have no current evidence of a population there. 'Teignmouth' tends to be applied to the area, not simply to the town; the records from Shaldon (apparently primary in Parfitt, 1889; probably secondary in Batters, 1902) may also have related to the same population. The names 'Torquay' and 'Torbay' have been used for large numbers of records from this area; although not helpful, their authenticity is not in doubt in the light of the many really accurately localised specimens and records from the same general area. These general records are fairly frequent over the period 1825–1932. The most northerly precise local records are from Tor Abbey Rocks. The name is now little used, but there is no doubt that it refers to either Corbyn's Head Rocks, or the large outlier, to the north on the other side of Corbyn Beach. This outlier is the more likely, since it forms the southern boundary of Torre Abbey Sands. Except for Harbreck Rock, well out into the Tor Bay, these are the only rocky outcrops near Torre Abbey.

Tor Abbey Rocks and Corbyn's Head Rocks hence form essentially the same location, although the former name has more often been applied; records, mostly specimens, exist for 1830–55, thereafter petering out. 'Torquay Abbey Rocks' (Grattann, 1873) is clearly another name for the same area, and the Salter record of 'Round Corbyn's Head . . .' must include Tor Abbey Rocks. Corbyn's Head Rocks still support (1971, 1972) a few colonies of *Padina* [Plate 2.] The plants are neither common nor easy to find, as they grow near low water level, in pools. *Padina* has quite probably been more prolific here in the past and may currently be in recession.

Livermead Sands, to the south of Corbyn's Head, form the southern curve of a small bay that terminates in the rocky Livermead Head. Livermead, Livermead Sands, and Livermead Rocks must all have related to the rocks below Livermead Head, also searched in 1971 and 1972. The probably much older population seems to have been sampled first in 1859, and most recently in 1971. The Livermead Rocks populations must be even more sparse than those on Corbyn's Head; neither on 22 September 1971 nor on 28 July 1972 could *Padina* be detected at Livermead. There seems currently to be general recession in *Padina* in this area.

In the Paignton area, records from Preston Beach probably relate to the rocky area at Hollicombe Head, which we have not examined. The records are all from that phycologically active era, 1872–92. Roundham Head, a similar rocky area south of Paignton Sands, may also have been lumped under Paignton. The area from Roundham Head south and east to Berry Head has been little examined in the past. This southern half of Tor Bay may sometimes have been submerged in the blanket term 'Torbay', but there is little basis for that assumption. The many coves and rocky areas along this coastline, especially Elberry [=Elbury] Cove, were widely visited by collectors like Holmes, Batters, and George in the period 1850–1900. Despite that, there is no record that can be firmly attributed to the area until that late season one established by E. Clay

Plate 2 *Padina pavonica* population in shallow pool near low water level, Corbyn's Head Rocks, Torquay, 28 July 1972. Photograph: W. D. Richardson.

(1953). A visit by one of us (W. D. R.) in September 1975 to virtually the same locality confirmed the presence of a few tetrasporic plants as a single clump in a silty upper shore pool.

The reasons why those from Brixham are the furthest western modern and authenticable records for the south coast are elusive; certainly, few data from localities further west are adequately supported on any basis now traceable. Holmes's (1906) area system resulted in a Plymouth record of *Padina*; Tregelles (1932) statement is based on that. There is an apparent (Plymouth) basis for the Holmes statement, in the regrettably undated specimen amongst a collection that contains many Brebner specimens bearing dates in the early 1900s. The general topic of far western records is reviewed below.

Cornwall

Eddystone Lighthouse:

Herb. Norman, 'procured from Eddystone Lighthouse. Purchased at Plymouth' (SUN).

Boscastle:

Holmes (1906*a*), one of the 'rarer species'.

General:

Morison & Bobart (1699, 1715, 1738), '. . . etiam è littore Cornubiensi collectam habemus' (as *Fucus maritimus Gallopavonis pennas referens* [Bauhin]).

Secondarily based on Morison & Bobart (1699) were: Dillenius in Ray & Dillenius (1724); Hill (1760) (as *Fucus fronde sessili reniformi decussatim striata*); Hudson (1762) (as *Fucus pavonicus*); Martyn (1763); Robson (1777); Camden & Gough (1789) (as *Ulva pavonia*).

Herb. HAMU, no other data; H. Boyden in Herb. W. R. Sherrin, no date, no other location (SLBI) – (Boyden's collections in SLBI are otherwise almost entirely from Cornwall, Scilly Isles.)

It is not clear why there are few records from any era, and no modern ones at all, for Cornwall; the general environment in certain Cornish localities does not differ radically from that of Devon areas where *Padina* is known. Other species present and available substrata closely resemble those in Devon *Padina* areas in, for example, Kennack Sands; between St George's Island and West Looe; near the estuaries of the Fal and Helford Rivers; and in shallow protected stretches in some of the small harbours in the south.

That the only precisely located *Padina* records derive from some of the at first sight more improbable Cornish locations is equally strange. Very strong wave-action appears likely to preclude growth of *Padina* on Eddystone. Drift, for reasons given elsewhere, seems only remotely possible. Labelling of the specimens seems unequivocal, but the phraseology '. . . procured from Eddystone Lighthouse . . .' is rather unusual. 'Purchased at Plymouth' may have indicated that the purchaser (Rev. Norman ?) had no direct information regarding collection, merely noting hearsay. This kind of situation usually produces inaccuracy and we view the record with scepticism. Boscastle, on the north-east, is an equally unlikely place from which to collect *P. pavonica*. The village is set well back from the shore and has a harbour approached by a winding, rather narrow cleft in the cliff; at intervals, particularly at the inner end toward the village, there are rather flatter lateral areas subject to rather less strong water-movement, although swell, current, and direct wave-action habitually create very rough water elsewhere in the approaches. It is difficult to conceive that Holmes would misdetermine other material as *Padina*, especially since the record was probably established from his own data; the annotation as to one of the 'rarer species' clearly indicates appreciation of the unusualness of the record. Several visits to Boscastle (J. H. P. 1974, 1975, 1978) did not reveal *Padina* in the inner reaches of the harbour. The terrain does not in any case encourage the expectation of locating the alga, although the possibility cannot be excluded; the relatively calm detrital conditions in which *Padina* best appears are virtually absent. We have to accept the Holmes record but, in the absence of supporting specimens, with reservations. For comments on the general paucity of north coast and Bristol Channel data, see below (Devon, North).

All earlier Cornish records depend on statements by Morison & Bobart (1699); the imprecise localisation did not prevent that original record being uncritically accepted and repeated over a period of virtually 100 years. It has to be admitted that there is a *Padina pavonica* specimen (unlocalised) in the Morisonian Herbarium [OXF] (Vines & Druce, 1914 : 223). Although this specimen was not enough to prevent the record thereafter slipping into obscurity, Bobart (who was responsible for the record in the first place) was not given to geographical inaccuracy and no doubt is expressed in his 1699 statement. Stackhouse, who knew well the coasts of Cornwall in the late 18th and early 19th centuries, did not mention the species and there are no relevant specimens amongst those with which he can be identified. Recent workers have never located specimens in Cornwall. Widespread observation (J. H. P.) on the Lizard and in West Penwith confirms the absence. For some unknown reason (perhaps that of breeding population size, discussed elsewhere), the alga apparently does not maintain itself in the far west of England.

Devon (North)

Ilfracombe:

ix.1837, Miss M. Williams (E).

This single record occurs in an area with many locations where finds of *Padina* would not be surprising. Watermouth harbour; parts of Hele Bay; the many mixed conditions of sand with rocky reefs off Ilfracombe itself; and Lee Bay, could all provide circumstances like those supporting *Padina* elsewhere. This reflects the rather larger general problem – that of the few reports of the alga in north Cornwall, north Devon, Glamorgan, and Pembroke, the general physical régimes in which are all essentially similar. Why are there so few records from the shores of the whole Bristol Channel, an area that (like both coasts of Cornwall) appears to embrace many potential local

habitats ? It is also curious that (cf. Eddystone and Boscastle, Cornwall) one of those very few records is from an area (Worm's Head, Gower; see below) of very considerable general exposure to wave-action.

Glamorgan

Worm's Head, Gower:

Herb. L. W. Dillwyn (BM).

This undated specimen was probably collected in the very early 19th century. Worm's Head itself is of firm rock, generally lacking detritus and exposed to seas of long fetch from the south-west. Superficially, it seems an unlikely habitat for *Padina*, but there are one or two small areas where low water level sand deposits have compacted onto the rock surface, providing the kind of conditions under which the alga often grows. Along the northern edge of the 'causeway' out to the island, muddy rocks emerge at low water. When searched, these rocks (SS 398873) did not reveal *Padina*. A common associate of *Padina*, *Taonia atomaria*, was growing on the north side of the 'causeway'. Three other small bays with similar detrital '*Padina* – conditions' [Fall Bay, Porteynon Bay (south side), and Oxwich Bay (south side)] could loosely be described as Worm's Head. We have been unable to examine these bays but (*teste* Drs Hayward and John) there are no recent observations of *Padina* from the Gower. It must be accepted that *Padina* could have appeared ephemerally on or near Worm's Head in the past; modern supporting data and specimens are desirable.

Pembrokeshire

Tenby:

ix.1930, Herb. R. Meinertzhagen (BM).

This comparatively modern record is an enigma. Many eminent 19th century shore workers visited Tenby, some (such as P. H. Gosse) many times and for long periods. None reported the presence of *P. pavonica*. This is no basis for outright rejection of a specimen-backed record, but there are other factors to be considered. Meinertzhagen collected marine algae widely here and abroad. Careful analysis of some unusual Kent records (specimens) from the Meinertzhagen herbarium has indicated that errors may well have occurred in the transcription of collection data from rear to front of mount sheets; there is, however, no direct evidence of such error on the Tenby specimen of *Padina*. Areas around Tenby (SN 145032) were examined carefully (1968, 1972) for the 'pools at low tide' described by Meinertzhagen. The rocks throughout supported rather poor growths of algae and nowhere could be detected the sort of conditions in which *Padina* could be expected to appear.

Anglesey

General:

Morison & Bobart (1699, 1715, 1738), ex *Insula* Anglesey (as *Fucus maritimus Gallopavonis pennas referens* Bauhin).

All the following entries are wholly or partly dependent on the original Bobart (1699) statement, although Davies (1813) could have added original observations (see text for comments on Davey, 1953):

Dillenius in Ray (1724); Hill (1760); Hudson (1762; as *Fucus pavonicus*); Robson (1777); Camden & Gough (1789; as *Ulva pavonia*); Davies (1813); Rees (1929; as *P. pavonia*); Davey (1953), '. . . Ray; Dav.; R. W. P. [hillips] . . .'.

Records for Anglesey seem to be extremely poorly authenticated. The only recent data depend on the 'R. W. P.' in Davey (1953), which is not supported by Phillips own (1898) work or herbarium specimens. Earlier records, traced back, all stem from Bobart (1699). As with the latter's Cornwall record, so has that from Anglesey been long repeated without supporting critical studies. There is as little real evidence for the existence at any time of *Padina* in Anglesey as there is for its

past appearance at Aberdeen. At least, in Anglesey, there seems not to have been interpretational error during data transcription.

Lancashire

Isle of Walney:

Hudson (1762), '. . . in littore Insulae Walney, sed rarius . . .' (as *Fucus pavonicus*).

This record is secondarily published in:

Martyn (1763); Robson (1777); Greville (1830); Batters (1902); Martindale, Holmes [& Batters] (1906, 1920).

Hodgson (1876, 1877), reporting collections from Furness, gave a description of shores around Walney: '. . . The high reaches of Morecambe Bay, as at Aldingham, Baycliff, and Ulverston, were always greatly influenced in their fertility by the position of the channel and the shifting of the sands. If the deep water ran up for a time on the east of Chapel Island, or at least pretty well out from these shores; then the old boulder clay (scars as they are called) would appear, washed from their thick covering of fine sand. . . . These long out-runners, or points, after re-exposure to light, air, and fine summer weather, are speedily clad with a rich verdure. Green and olive coloured plants of the most delicate structures fringe the small tide-pools, barely getting time to mature their loveliness ere huge bosses of tangle come and contest the ground. . . .'. Consolidated boulder clay surfaces could well have supported ephemeral growth of *Padina*. They are very like the substrata at, for example, Bembridge (Isle of Wight), where plants grow well. Hodgson (1876) was already not prepared to say '. . . whether there is much favourable ground for the study of marine botany on the coast of Furness now . . . Clean, sweet waters, with but a moderate supply of mud are essential conditions to the growth of these beautiful plants, and in this respect Roa Island had some time ago greatly fallen off . . .'. More than a century earlier, when the single known original record was established, conditions were probably rather better. Hudson had some as yet unidentified but definite connection with the Isle of Walney; he knew the circumstances of the *Padina* there reported sufficiently well to add confidently '. . . sed rarius'. We accept, in the absence of contrary proof, that this could have been a chance fleeting occurrence in the same category as the recent find by Cullinane in Fennels Bay, Co. Cork (*q.v.*). Ketchen (1965 : 23) indicated that, even recently, many brown seaweeds (not naming *Padina*) are on Walney Island attached to stones in the littoral or thrown up in drift. The possibility of future ephemeral finds of *Padina* is therefore not excluded.

Ayrshire

Ayr:

in Coll. J. MacNab, not dated [mid 19th century] (DBN).

Ayrshire coastlines are essentially sandy, but there are rocky outcrops at Prestwick; north of the mouth of the River Ayr; and, especially, forming the south side of Ayr Bay from near Doonfoot down to the north side of Culzean Bay (Heads of Ayr). Ephemeral stabilisation of detritus tolerable to *Padina* could therefore occur. After substrata, primary factors of importance to *Padina* seem to be the levels of insolation and temperature. Locally accurate treatment of the effects of these parameters is not feasible; apart from sheer lack of data about shore environmental parameters, as Russell (1973) has recently indicated, studies in benthic marine ecology are on the whole not sufficiently sophisticated to identify precisely the environmental causes of biological events. Generally, this Ayr record, one of the most northerly after those from Aberdeen (discounted) and Argyllshire (drift and doubtful), is the only one from an area with mean August sea surface temperature below 14 °C. Wade's Connemara record (see Co. Galway) is the only other from an area with mean August temperature below 15 °C, and that record is also doubtful. Ayr lies in the coastal area with average summer sunshine hours lower than elsewhere in the British Isles. By contrast, major British populations of *Padina* occur in areas where (i) mean sea surface temperatures are generally greater than 16 °C (August) and average maximum summer air temperatures are greater than 20 °C; (ii) average summer sunshine hours are greater than elsewhere in the British

Isles. On these grounds alone, *Padina* records from Ayrshire cannot be totally discounted since, apart from other considerations, the environmental data derive from adjacent open sea, not coastal, conditions. However, ephemeral occurrence of local conditions tolerable to *Padina* is likely to be a rarer event in Ayrshire than in the more favoured southern areas. With considerable reservation, since firm evidence against the record is lacking, we must accept this as a rare occurrence that currently constitutes the known northern limit of the species, as based on extant specimens.

Argyllshire

Machrihanish Bay [Kintyre]:

Lothian (1862), late December/January, drift.

The record was based on material picked up from vast heaps of drift along the tide-mark, most of it fresh and sent in by the preceding day's gale, some actually from the last tide. The statement about *P. pavonica* expressed no doubt, but the list was terminated by '. . . with many others which memory fails to furnish'. Reservation remains about this most northerly record on the western coast since (a) drift *Padina* is rare in Britain (see elsewhere); (b) it is an especially odd time of year for so northerly a location; (c) substrata on Kintyre are not hospitable – shingle beaches and rocky outcrops run down most of the western coast, whilst at Machrihanish there is a long curve of sand backed by dunes; (d) there is no material to support this record clearly based on memory after the event. Confusion with other species (? *Taonia*) is likely.

Ireland

Co. Galway

Near Aughris, Cunnemara [*Connemara*]:

Wade (1804), as *Ulva pavonia.*

Padina '. . . was found sticking to the sea rocks . . .'. For general environmental comment, affecting the credibility of the record, see Ayrshire, which presents a similar situation. The Co. Galway record is even more doubtful than that from Ayr, since it is not based on an extant specimen. Cullinane (1970 : 278) was unable to find material that could be proved to have connection with Wade, or to be from this locality. The record must therefore be viewed with doubt, but see the discussions later.

Co. Cork

Fennells Bay, near Myrtleville, Cork Harbour:

shallow rock pool near MLWS, Cullinane (1970; *1971*; *1973*). Specimen presumably in CRK.

This material, the only authenticated *Padina* from Ireland, was collected by Cullinane from a south-facing shore in Cork Harbour, where it was growing in a rock pool. The single small specimen, correctly determined, has been seen by one of us and is dated May 1968, despite the (1970) statement that it was collected in 1967. Guiry (*pers. comm.*) examined the same area, including the precise spot, described to him by Cullinane, in 1971 and August, 1973; no specimens of *Padina* were detected. The 1968 find therefore provides a prime example of an ephemeral growth in an unusual area, in conditions by chance tolerable; similar growths will probably eventually occur in sheltered detrital circumstances elsewhere in the south of Ireland. This is not an original forecast; Harvey (in Mackay, 1836) commented that *P. pavonica* '. . . one of the most remarkable of British algae, has not yet been found on our [Irish] shores; but it may be expected to occur on the southern coasts of Cork or Waterford'.

Distribution along adjacent continental coasts

This analysis is not as complete as that given for British *Padina*. Information has been assembled up to the point when a consistent framework emerged, and that used for comparisons. General trends in space and/or time on the Dutch, Belgian, French, Spanish, and Portuguese coasts have so been identified, and related to past and present events concerning individuals or populations on the British coasts. The patterns that emerge from continental data are still dependable; where

peripheries of the apparent distribution have been involved (Netherlands and Belgium), or where critical inconsistencies seemed to be emerging, analysis has been as detailed as for Britain. There is locally an absence of modern data very similar to that noted for parts of the British coasts; the parallel extends to a similar distribution pattern where data *are* available (Fig. 1).

Benelux

Drift material sometimes occurs in Belgium and the Netherlands, despite the usual disintegration of plants *in situ*. If reports can be accepted, this was the source of the record in virtually every occurrence of *Padina* along Dutch and Belgian coasts. Apart from that, tracing back through records and specimens reveals a very small number of authenticated primary observations of even drift material. The Belgian pattern of records (see following section) is thus essentially similar to the Dutch. There are no naturally rocky or firm substrata along the coasts of the Netherlands and Belgium; sand is predominant, with strong intermixtures of mud in, e.g., the estuary of the Scheldt, where river debris are significant. Den Hartog (1959) emphasises the great importance of artificial substrata in the benthic marine ecology of the Netherlands, and Belgium, although less complex because shorter, has an essentially identical situation. There are a few cases in which detritus over firm artificial substrata exists or existed in the Netherlands, e.g., the Scheldt and parts of the Grevelingen, now sealed against the sea. Nienhuis (1968, 1969, 1970, 1972) made detailed long-term studies of such areas, but never detected *Padina*; by contrast Boddeke (1957, see below) reported the alga from the Oosterschelde.

Netherlands

Oosterschelde:

Boddeke (1957) '. . . *Padina pavonia* en *Taonia atomaria* slechts enkele malen gevonden zijn.' [=were found only a few times.] Record repeated in Dresscher (1976).

Scheveningen:

Gorter (1781), '. . . Te Scheveningen aan't Strand. (MEERBURGH) . . .' (as *Ulva pavonia*).
Secondary (drift: Scheveningen) records based only on Gorter are:
Houttuyn (1783); van den Bosch (1853); Suringar (1870; possibly unjustly regarded as wholly secondary); van Goor (1923); Bremer (1943); Lucas (1950).

Netherlands general:

Bosch (1851). Record repeated in Dresscher (1976).

Den Hartog (1959), plant '. . . of southern origin that . . . [is] . . . washed ashore on the coast of the Netherlands . . .'. (Not clear whether this is supported from his own, or entirely dependent on previous, data.)

The only certainly original Scheveningen record is that in Gorter (1781). The Meerburgh whom Gorter (p. 318) credited with the collection was apparently (p. iv) then the first gardener in the Leiden University Garden. He collected many rare plants in the Netherlands, all being passed to Gorter. *Padina* was presumably drift, from the phraseology employed; subsequent authors have concluded so. Houttuyn's report, not acknowledged as from the same source, is so close in time, phraseology, and localisation that it must surely be at least largely a secondary reference. Neither can be confirmed from material, and no additional original unpublished data have been traced. There are no specimens of *Padina* from Dutch European shores in the Leiden collections. This fact also leaves reservations about the record from the Oosterschelde, since the statements by Boddeke lack precision; however, appropriate habitat conditions were hitherto available in the area concerned (see above).

Belgium

Oostende:

Kickx & Kickx (1867), attached to stones thrown up on the beach and on parts of piles tidally

uncovered by the sea, Ostende and Nieuport; Herb. Hort. Belg., Fr. Crépin, received June 1877 (K in BM); Westendorp & Waller, *Herb. Crypt. Belg.*, no. 1335 (as *Zonaria pavonia*), only found as fragments thrown up on the beach at Ostende, young ⊕ (K in BM; BM).

Secondary records quoting Kickx & Kickx: De Wildeman (1896); De Wildeman (1898); van Heurck (1908).

Secondary record quoting Kickx & Kickx and Westendorp & Waller: Chalon (1905).

Niewpoort:

Kickx & Kickx (1867), as Oostende, above.

Secondary records quoting Kickx & Kickx are: De Wildeman (1896, 1898); Chalon (1905); van Heurck (1908).

Belgium general:

Lestiboudois (1781), Flandres (included in 'Provinces septentrionales de la France'); Roucel (1803), Nord de la France (from title), Flandres (from vol. I, Introduction), on the sea-coast attached to stones and shells; De Wildeman (1896), Flandres occidental; Lyle (1923), Flanders (assumed Belgium and France); *van Goor* (1923), Black Sea to southern England and Belgium.

The Belgian coast, as indicated earlier, offers hardly even the slightest expectation of encountering established *Padina*, and it is no surprise that there are few records. Only two unequivocal, authentic, cases have been traced: those of Kickx & Kickx (1867; the earliest) and of Westendorp & Waller (received in BM June 1877, record undated). The similarity of data between the latter and the Crépin specimen (see above) indicates that the same collection was probably involved. Specimens to support the Kickx & Kickx record may exist in Brussels, but we have not seen them. Kickx & Kickx's use of 'pilotis' [=piles] presumably relates to vertical supports of groynes, an unusual but possible substrate for *Padina* if there was fairly consistant detrital cover around the base. The report from stones thrown on the beach is somewhat surprising since that now rarely occurs (see elsewhere); long distance drifting of *Padina*, even in its very early growth-stages, cannot have been involved. The Westendorp specimens were from a very similar period to the statement in Kickx & Kickx and support its authenticity; available data and appearance of specimens suggest more fully grown material, possibly carried north and east by residual currents along the French coast. All subsequent records, whether general, from Oostende, or from Niewpoort, are secondary.

Fig. 2 The distribution and limits of coastal divisions along adjacent continental shores. Départements in France; provincias in Spain and Portugal.

France:	1. Nord	Spain:	18. Guipúzcoa
	2. Pas de Calais		19. Viscaya
	3. Somme		20. Santander
	4. Seine Maritime		21. Oviedo
	5. Eure		22. Lugo
	6. Calvados		23. La Coruña
	7. Manche		24. Pontevedra
	8. Ille-et-Vilaine		
	9. Côtes du Nord	Portugal:	25. Minho
	10. Finistère		26. Douro Litoral
	11. Morbihan		27. Beira Litoral
	12. Loire Atlantique		28. Estremadura
	13. Vendée		29. Baixo Alentejo
	14. Charente Maritime		30. Algarve
	15. Gironde		
	16. Landes	Spain:	31. Huelva
	17. Basse Pvrenées		32. Cadíz

This outline map is not orientated precisely north←→south; it has been taken for convenience from the National Geographic Society's Chamberlin Trimetric Projection.

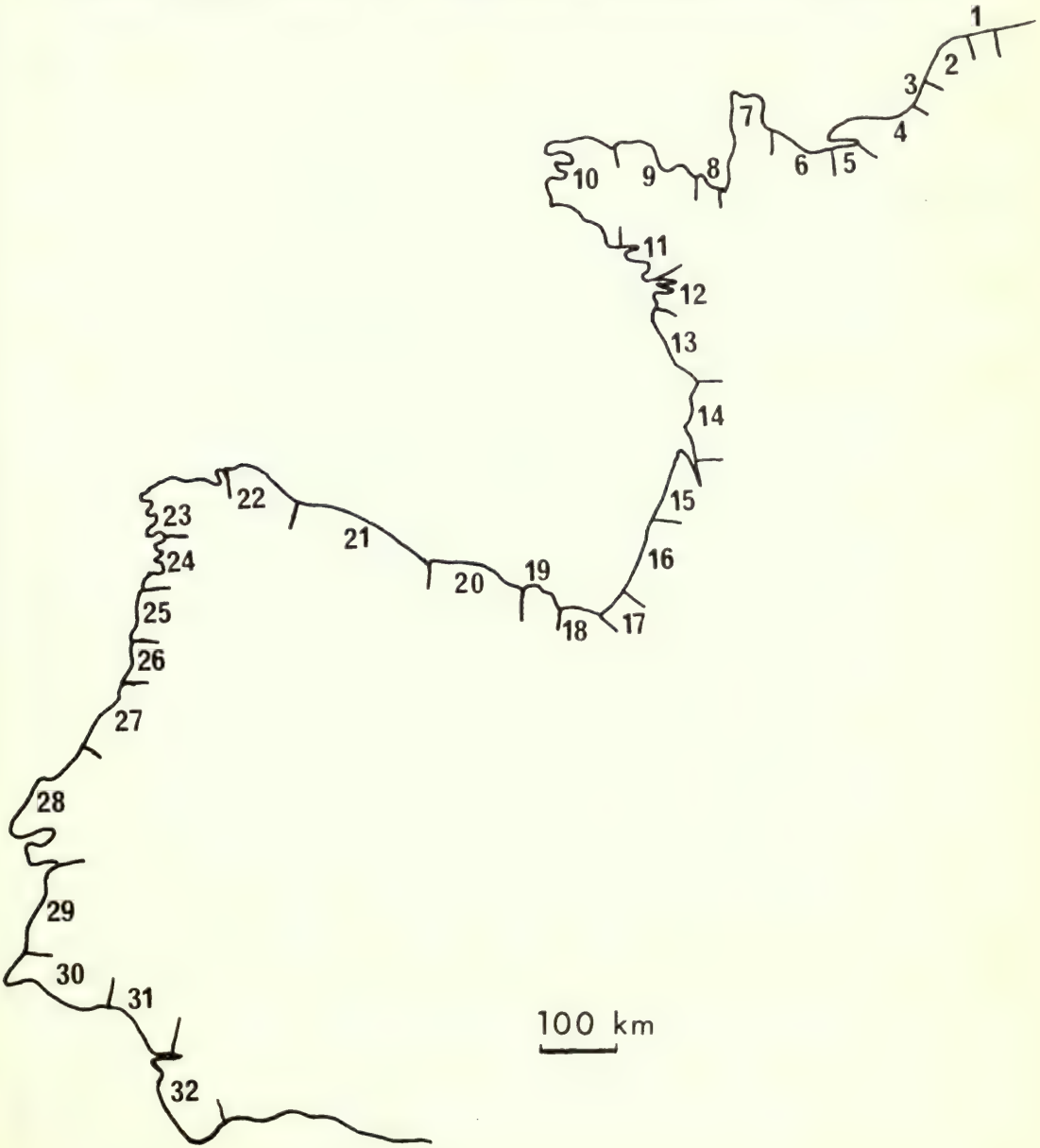
Lestiboudois (1781), whose '. . . Provinces septentrionales de la France' must be taken to cover the whole of Belgian and French Flanders, has the earliest traced record. Later (1827), he localised his *Padina* record precisely to Dunkerque (Nord); this French area may therefore have been the real source, at least in part, of the earlier general record. Roucel's (1803) record, despite absence of acknowledgement, is certain to be repeated from Lestiboudois (1781) and is therefore cited for Belgian Flanders.

France

General

Under various names (*Ulva pavonia; Dictyota pavonia; Padina pavonia*), the species has been recorded in general terms for France by:

Lamarck (1779); Lamarck & De Candolle (1806); Lamouroux (1813); Desmazières, *Pl.*



Crypt. France, ed. 1, sér. 1, 1825–51; Desmazières, *Pl. Crypt. France*, ed. II, sér. 1, 1836–51, no. 1108; Duby (1830); van Heurck (1908); Hohenacker, *Arzn. und Handelspfl.*, no. 215; and in Herb. Ph. Hepp (BM).

It is not possible to attach a great deal of importance to records so general that they cannot even be identified at the geographical level of département; almost always, these records are a distillation from extant data and often gloss over a lack of real information. Citation here is solely to establish that potential sources of important information have not been overlooked. More recent French works with general records yield useful data on reproductive and vegetative phenology (Feldmann, 1937, 1938; Hamel, 1939; Gayral, 1966). For the distribution of the divisions of France, Spain, and Portugal employed, see Fig. 2.

Nord [French Flanders]

Dunkerque:

Lestiboudois (1827), '. . . A Dunkerque, sur les coquillages, etc. . . .' (as *Dictyota* (*Padina*) *pavonia*).

Secondary records quoting Lestiboudois:

Moniez (1880); Debray (1883*b*); Debray (1899); Chalon (1905); Cozette (1911).

Flandres general:

Lestiboudois (1781) [1799, reported new edition, not seen: may more correctly be listed under Dunkerque], on the sea-coast, attached to stones and shells (as *Ulva pavonia*).

Secondary records quoting Lestiboudois:

Roucel (1803); De Wildeman (1896); Lyle (1923; probably based on Dunkerque records and the early general ones).

General records citing Flanders have been taken to refer equally to both Nord (French Flanders) and Belgium. Lestiboudois (1781, 1827) provides the basis for this assumption; his earlier title '. . . les Provinces septentrionales de la France' was subsequently altered to '. . . nord de la France, et de la Belgique proprement dite'. Essentially the same conditions of physical environment apply as for the Netherlands and Belgium (*q.v.*). As in those countries, all records for Nord refer back to a single early statement, in this case from Lestiboudois (1781). Similarly, the records localised to Dunkerque depend on the slightly later statement by Lestiboudois (1827). Neither 'pierres' nor 'coquillages' are common substrata for *Padina*, although when set in and covered by firm detritus there seems no good reason why shells should not form a substrate at least as acceptable as 'pilotis' (Kickx & Kickx, 1867; Belgium).

Pas de Calais

Wimereux:

Moniez (1880), thrown up twice near la Rochette.

Secondary records quoting Moniez: Debray (1883*b*).

Secondary records quoting data from Giard (see below) and Moniez: Debray (1899); Chalon (1905); Cozette (1911).

Pas de Calais general:

Lyle (1923).

The coast of Artois (= Pas de Calais) has detritus-covered boulders, either at low water level or in standing pools at various levels, near Cap Gris Nez and locally elsewhere. Nevertheless, Wimereux is the only location recorded; currently, it possesses much solid detritus-covered substrata, formed by a large area of upper shore cultivation pools south of the Wimereux Laboratory. Opening of the latter in 1873 was probably the cause of a spate of records shortly afterwards. Seaward and slightly north of the pools, a large area of shattered concrete boulders,

perhaps old wartime defences, reaches down virtually to low-tide level. Thickly covered by slimy detritus, the boulders retain standing water at intervals; their surfaces are often well-shaded and damp, even when above standing-water level. The boulder area, and shallow mud/shingle based large pools at its inshore fringe, form a suitable environment for *Padina*, but none was detected during careful examination in 1971 (J. H. P.; I. T.). Likely areas on and near Cap Gris Nez, and elsewhere between Calais and Boulogne, were also unproductive. This lack is enigmatic; it could be taken as a recession period, but that would not account for the similar absence of earlier records, other than of drift plants, for the area. Strong wave-action and fetch may be a part-explanation, since the English coast analogue of the Artois projection is the South Foreland which, rather less directly affected by long fetch, still lacks a satisfactorily established history of early or recent *Padina* records and carries no current populations (Price & Tittley, 1972).

We have been unable to locate the 'Giard' source mentioned by both Debray and Chalon; Giard was at this time Director of the Wimereux laboratory, so that specimen labelling or verbal communication may have been involved.

Somme

No traceable records for the area.

Since they are beyond the usual northern limits for consistent presence of *Padina*, the continental areas so far dealt with (Pas de Calais; Nord; Somme; Netherlands; Belgium) constitute the analogue of Essex, the Thames Estuary, Kent, and East Sussex.

Seine Maritime

St Jouin:

Debray (1899), flat rocks, middle zone, based on Bernard (unpublished – see text); *Chalon* (1905), Bernard; Coulon (1912), pools, summer–autumn; *Mail & Senay* (1957), Bernard, '... Espèce fugace . . .'.

Étretat:

Wuitner (1921, 1946), in le Chaudron; *Mail & Senay* (1957), middle zone, au Chaudron, '. . . Espèce fugace . . .', based on Wuitner.

Fécamp to Pointe du Hoc, general:

Mail & Senay (1957), rare, '. . . Espèce fugace . . .', E. [bran], quoting from his unpublished catalogue.

Attached material has been recorded, but rarely; Seine Maritime and Pas-de-Calais have much in common, since apparently ideal locations lacked and still lack plants. The area on the north side of Fécamp Harbour (J. H. P. and I. T.; September 1972) is typical of these; flanked by shingle, the location itself is of low boulders and flat slabs, the latter much eroded into declivities and hollows, with standing water and muddy detritus. *Taonia atomaria* was luxuriant and abundant, but *Padina* was absent. Plants were also then lacking from Étretat area, although reported there by Wuitner in 1921. Ebran and Bernard, the original sources of data quoted for this area, were local botanists whose lists of marine algae were never published, although Ebran produced a catalogue of vascular plants for the region of Le Havre and Bernard published a field excursion report which referred generally to algae. Bernard was said to have inherited Ebran's algal list and incorporated his own data with the intention of publication (Mail & Senay, 1957).

Eure

No precisely located records:

Normandie general*:

Lyle (1923); Chauvin in Suringar, in Herb. Weber-van Bosse, on rocks, all Normandy coasts

* A name of variable application; we have taken Normandie to include Eure, Calvados, and Manche. Some authorities also add Ille-et-Vilaine, which we have included in Brittany.

(MS Chauvin), 937.55.397 and 937.156.64 (L); Chauvin, J. (1827), *Algues de la Normandie*, fasc. 1, no. 23, on rocks, all along the coast, July–September.

Fécamp to Pointe du Hoc, (*Calvados*):
Mail & Senay (1957). See Calvados.

Calvados

Luc:
Crié (1875), rocks at MTL; Chemin (1923), end July and August, MTL, muddy surfaces, ⊕; Hamel (1939), Lamouroux; Hohenacker, *Alg. mar. sicc.*, 1852–62, no. 25, ⊕ (BM; also Herb. Suringar in Herb. Weber-van Bosse, L 937.55.407 and 910.161.569); undated, localised in MS Lenormand (L 937.55.336).

Quihot:
Debray (1899); *Cozette* (1911).

Langrune:
Debray (1899); Chalon (1905); *Cozette* (1911); Chemin (1923), end July and August, MTL, muddy surfaces, ⊕.

St Aubin:
Chemin (1923), details as Langrune (*q.v.*).

Arromanches:
Crié (1875), rocks at MTL; Pelvet in Herb. Hepp, juvenile ? ⊕ (BM); sin. num./loc./ann., ⊕ (K in BM).

Bouffay:
Plessis (1961), hollows with continual fresh-water inflow, very dense populations but always very local in Calvados, the very few colonies being transient.

Port-en-Bessin to Bouffay:
Plessis (1961), several transient colonies at foot of cliff in the *F. vesiculosus* level.

Port-en-Bessin:
17.ix.1879, coll. Bertot, plage, ⊕, Herb. Héribaud Joseph (BM; K in BM); Debray (1899); Chalon (1905); *Cozette* (1911); *Hamel* (1939) (Bertot); coll. Elise Verrier, sin. loc./num. (TCD).

Pointe du Hoc:
28.vii.1965, three plants, coll. Serajuddin, ⊕, P88/1/– (PLTH).

Grandcamp:
Debray (1899), common; Chalon (1905); *Cozette* (1911); Gayral & Bert (1966).

Calvados general:
Roussel (1806), 'submarine'; *Hamel* (1939) (Chauvin, *Alg. Normand.*, no. 23); Suringar in Herb. Weber-van Bosse, 937.55.409 (L); Pelvet, as *Zonaria pavonia*, 937.55.410 (L); R. J. Shuttleworth, ⊕ (BM).

Fécamp to Pointe du Hoc:
Mail & Senay (1957), rare, '... Espèce fugace ...', E. [bran]. (See comments at Seine Maritime.)

Normandie general records:
See Eure.

Reports exist of attached plants immediately north of Le Havre and therefore still in Baie de la Seine; frequent and dense (however ephemeral) populations seem not to commence until the inner reaches of the Baie, west of the Orne Estuary. Early Calvados records are not precisely located; Roussel's (1806) record (title localisation only) is the earliest traced. All other general records are supported by material; although none is dated, those from Pelvet and Chauvin are clearly mid-19th century. Probably these poorly documented records were all from west of the Orne. None have been traced from the phycologically little-known area between the Orne estuary and the Calvados eastern limit, near Honfleur. Mail & Senay (1957) included in their catalogue the area west to Pointe du Hoc (near Grandcamp) because, from Fécamp to the Seine estuary, the south bank of the Seine was so poorly known. We have no records localised exactly to Eure for that same reason. Records listed at Eure (*q.v.*) are included only because they are general to Normandie, or to the area covered by Mail & Senay. The south bank of the Seine, over the whole of the area west to beyond the Orne, is strongly estuarine in character. The Seine itself (of immense influence), the Orne, the Dives, and the Touques estuaries strongly affect local conditions and the substrata are almost all mobile – sand, mud, or sand/mud/alluvium mixtures. Apart from local artificial constructions, the major exception is the rocky area stretching from les Perques de Villerville south for some 4 km to the northern outskirts of Trouville (Rochers des Creuniers) and there is a smaller rocky beach west of Villers-sur-Mer; no previous *Padina* data exist for either rocky area.

West of the Orne estuary, rocks with occasional large associated inshore sandy stretches commence at Lion-sur-Mer; except for short interruptions between Graye-sur-Mer and Arromanches, and around Saint Laurent-sur-Mer, these are continuous to the east bank of Baie des Veys (Rochers de Grandcamp). A recent detailed study of this previously well-collected area (Plessis, 1961) gives more information.

The Côte de Nacre (Orne to Arromanches) and the western portion from Arromanches to Grandcamp (Bessin) form a calcareous coastline which is relatively sheltered; Cotentin Peninsula reduces the effects of dominant winds from the west. Foreshores from the Orne to Arromanches are wide (2 km or more) at low water. Tidal amplitude is considerable and, because the flood is much stronger and faster than the ebb, sediments tend to be carried west to east, despite the Seine outflow. Westward, except for the Rochers de Grandcamp, the intertidal is much narrower.

Padina habitat requirements and periodicity are very similar throughout this area, although records exist for only a few places. Luc-sur-Mer, about 10 km west of the Orne, is probably best known, being the location of the Marine Laboratory, Université de Caen. Plessis (1961) did not record *Padina* from either the Côte de Nacre or Luc, despite studying in detail many of the rocky areas, such as the well-known le Quihot, very near to the Laboratory and specifically mentioned for *Padina* by Debray and (secondarily) by Cozette.

Manche
St-Vaast-la Hougue:
viii.1841 (MS Lenormand), 937.150.142 (L); Chalon (1905), Herb. J. B. de Bruxelles; Hariot (1912), on stones in sandy pools, summer, autumn; Herb. Buse de Brébisson, no. 360 (MS Lenormand), 910.161.565 (L).

Île Tatihou:
Wuitner (1911), Passage du Rhun; Hariot (1912), not very widespread at Tatihou, le Rhun, near the jetty, behind the fort, summer, autumn; Wuitner (1921, 1946), passage du Rhun, (Tatihou), summer, lower shore, rather common; Hamel (1939), passage du Rhun (Lebel); 30.vii.1965, G. T. Boalch, '. . . Present in such abundance that it crunched as we walked along the causeway to Tatihou . . .' (*pers. comm.*); Gayral & Bert (1966), 26–31.vii.1965, same meeting as Boalch record above.

Cap Lévy:
Gayral & Bert (1966), 26–31.vii.1965.

Barfleur:
Chalon (1905), Herb. J. B. de Bruxelles; *Cozette* (1911); Chemin (1934*b*), in the transition area between sands and the mud, rather common, but *Taonia* much rarer.

Cherbourg:
viii.1827, ⊕, Le Jolis in Herb. Dickie (BM); viii.1828, Fischer in Herb. R. J. Shuttleworth (BM); 10.ix.1836, Le Jolis (TCD); 1.ix.1856, Bornet (DBN) (937.55.400, L); 16.ix.1856, ⊕, Le Jolis (K in BM); 7.x.1858, Le Jolis in Greville Coll., no. 1450 (E); Le Jolis (1863, 1864), peninsula can be regarded as one of the most northerly stations of *Padina pavonia*, on stones in shallow MTL pools, summer, autumn, common; Crié (1875), common; Stenfort (1877), widespread and rather common, summer, autumn; Chalon (1905), midlittoral, Le Jolis; *Cozette* (1911); *Hamel* (1939), Thuret & Bornet, Le Jolis, *Alg. Cherb.*, no. 77; Le Jolis; viii, *Alg. mar. Cherbourg*, no. 77, ⊕ (BM; 937.55.418 & 937.150.75, L); Lenormand in Herb. E. George (BM); Herb. R. J. Shuttleworth, ⊕ and sterile material (BM; K in BM).

Querqueville:
8.ix.1907, Herb. Corbière, 960.113.744 (L).

Blainville:
Meslin (1925), on rocks in sandy rock pools with running fresh-water, MTL, ix.1924.

*Îles Chausey**:
Crié (1875), rocks at MTL; Hamel (1938), ix.1937; Davy de Virville (1938), (i) Saccaviron, Grand Île – depression between the adjacent reefs la Meule and Île-aux-Oiseaux has large pools at different levels, with sand/gravel bottoms, joined by constantly flowing runnels studded with rocks, bases of large deep upper pools, and inwash channels with small pools, have abundant *Padina*, (ii) Petit-Êpail (islet south of Grand Île) shows shallow hollows, containing sandy pools with consistent seawater trickles and bearing *Padina*; Hamel (1939); Hamel & Lami (1972), rather rare, Saccaviron, vi–ix.

Granville:
Crié (1875), rocks at MTL; Chalon (1905), Herb. J. B. de Bruxelles; *Cozette* (1911); *Hamel* (1939), Pelvet; Davy de Virville (1952*b*), Point du Roc [Cap Lihou], sheltered rocks below town, south of point, already affected by Baie de Saint-Michel mud, comparison of autumn 1937/spring 1938 with 1952 shows pools with *Padina* no longer exist – impoverishment of flora is accompanied by loss of coastal fauna, with grave scientific/practical consequences, severe regulation of collecting and cutting of algae required as remedy; Gayral & Bert (1966), 26–31.vii.1965; ? Pelvet, in Suringar in Herb. Weber-van Bosse, 937.55.411 (L).

General:
See Normandie general records at Eure.

Manche (mainly due to Cotentin) has the second longest coastline, after Finistère, along Atlantic France. The north↔south orientation of Cotentin gives three different major aspects, east (Baie de la Seine); north (English Channel); and, longest by a factor of three, west (into the Passage de la Déroute, between the Channel Isles, and into the Golfe de St Malo). Distribution of *Padina* records, although possibly affected by collecting habits of phycologists, largely reflects the

* Îles Chausey, about equidistant from Granville (Manche) and Pointe du Grouin (Ille-et-Vilaine), are often included (e.g. Hamel & Lami, 1930) in Ille-et-Vilaine.

presence of areas sheltered from long Atlantic fetch into the English Channel from the west. Three record groups are evident:

(a) the Saint-Vaast–Tatihou–Barfleur area of the east-facing coast;
(b) the Cap Lévy–Cherbourg–Querqueville area of the northern Cotentin coast, sheltered from fetch by Cap de la Hague; and
(c) the Blainville–Chausey–Granville area of the southern half of the long west-facing coast, protected from fetch by being well within the Golfe de St Malo.

These groups of records also reflect the main areas where cliffs and rocky foreshores abut stretches of low water sands, giving shallow detrital pools. On sandy east Cotentin, rocks occur at Hameau and Quineville; further north lies the classic area of la Hougue and Tatihou. From Saint-Vaast-la Hougue to Barfleur the coast is low, with rocky platforms (reefs) covered by dense algal growths. Saint-Vaast and Tatihou show slightly stronger wave-action than elsewhere in the vicinity (Fischer-Piette, 1932) but there is no really wave-beaten rock surface. Granitic rocks occur along the north coast from Pointe de Barfleur (Gatteville) to Cap Lévy; outcrops are at first isolated in a primarily sandy shore, but about Cosqueville become more continuous, below cliffs. From Cap Lévy to Cap de la Hague, the east↔west trend of the northern coast is roughly maintained, the cliffs descending westwards, towards sandy Urville. West again, other high cliffs terminate just before the low granite promontory of Pointe de Jardheu. Western coast headlands are mainly of more resistant rocks, and the long (more than 1 km) Pointe du Roc; the town of Granville, at the entrance to Baie du Mont St-Michel, stands on the latter. Between these two major headlands, wide belts of sand dunes occur, with intermittent wide rocky reefs bordering them to seaward.

Local presence of tolerable substrate conditions has been emphasised, since so important to *Padina*. Other environmental aspects are unlikely to restrict *Padina* distribution here; Cabioch (1969) maps many such aspects for areas west of Cherbourg. Local abundance of areas in which *Padina* could be expected to occur indicates that past collecting patterns must have strongly influenced the mosaic availability of data. The long history of collection and observation from Saint Vaast-Tatihou reaches back at least to 1831 (see Hariot 1912 : 2–3 for an historical summary); collecting in that area was stimulated by the foundation (1881) of the Laboratoire de Tatihou. Cherbourg area is well known, mainly through visits by Thuret (1846, 1850, 1863, 1866, 1874, etc.), accompanied by Bornet from 1852 onwards. Le Jolis, born and resident in Cherbourg, studied with Bornet and Thuret; both gave considerable help with his *Liste des Algues marines de Cherbourg* (1863, 1864, 1880). Bornet, Thuret, and Le Jolis also frequently visited the Saint-Vaast area, although Le Jolis is said to have preferred Cherbourg for algae. *Padina* data for Granville area were initially recorded by Pelvet, important comparative information being later provided by Davy de Virville. Harvesting of algae seems then to have been causing deleterious effects on *Padina* and the whole littoral ecosystem. Current comparative data are now required.

Channel Islands

Alderney:

Fort Houmet: Marquand (1901); *van Heurck* (1908), pool near there.

General: C. B. W. Brook, seven plants, one 29.viii, two others 19.ix, rest undated, all ⊕, acquired 8.vii.1920 (BM); Lyle (1920); Chemin (1934*b*), great development of rocky shore facies algae at all levels, muddy facies flora very rare to non-existent, *Padina* reported by Marquand, *Taonia* not at all.

Guernsey:

L'Ancresse: Lyle (1920).

Port Soif: 5.ix.1960, D. Hepper, four plants, all ⊕, P88/1/11 (PLTH); Dixon (1961), 5.ix.1960.

Grandes Rocques: Marquand (1895, 1901); *van Heurck* (1908); Dixon (1961), lower midlittoral and sublittoral, ix.1960, D. Hepper (Ballantyne).

Cobo (*Long Rock*): Dixon (1961), lower midlittoral and sublittoral, ix.1960.

Cobo: 10.viii.1883, E. George, in bay (BM); 25.ix.1893, 31.viii.1894, E. D. Marquand (NMW);

Marquand (1895, 1901); *van Heurck* (1908); *Lyle* (1920); D. Hepper (Ballantyne), in bay.

Albecq: Lyle (1920), ex Marquand.

Vazon: Lyle (1920).

Rocquaine Bay: Marquand (1895, 1901); *van Heurck* (1908).

Portelet: Lyle (1920), ex Marquand.

Côte Est (*Belle Grève Bay*): Davy de Virville (1963), in lower large flat pools, infrequent on these islands.

Côte Nord-Ouest: Davy de Virville (1963), only here and there in sandy pools.

General: viii.1840, ⊕; ? Crié (1875); Batters (1902).

Herm:

South end of Shell Beach: Dixon (1961), ix.1960, lower midlittoral and sublittoral; Feldmann (1961), sandy rocks; Davy de Virville (1963), ix.1960, in small pools.

Jersey:

Near Mt Orgueil Castle: ix.1835, Herb. W. C. Trevelyan (HAMU); ix.1835, A 415 (UCNW); ix.1835, Dr Jermyn in Herb. R. H. Meldrum (E).

Tour Seymour: van Heurck (1908), '(1903 Bov. Lap.)' [=R. P. Bovier-Lapierre].

Baie de St Clement: Miss Dyke Poore, 8.x.1859 (BM), ⊕; van Heurck (1908) (Piq.) [=John Piquet].

Pontac: 31.vii.1883. 18.vi.1889. E. George. ⊕ (BM).

St Helier: Ralfs (1842), two places near there, Miss White.

Near Elizabeth Castle: vii.1883, F. S. in Herb. Batters, ⊕ (BM).

St Brelade's Bay: G. E. Morris, ix.1957, midlittoral pools, ex Herb. Liverpool Univ. (GL).

Grève de Lecq: viii.1843, Herb. J. Dickson (E); viii.1848, Herb. M. White, 'Gave de Lacq' (TCD).

General: 1835, Dr Jermyn in Herb. R. H. Meldrum (E); viii.1843, Herb. Dickson (E); Harvey (1847, pl. 91), Miss White and Miss Turner; J. Cocks, *Alg. Fasciculi*, Feb. 1855, pl. 36, fasc. iv, midlittoral shallow sandy pools, viii and ix, ? ⊕ (K in BM; BM; PLTH); 1857, Jersey (BKN); *c.* 1860–1, 'Aunt Mary', ⊕ and sterile, P88/1/12 (PLTH); Johnstone & Croall (1860); Plues (1864), Jersey; Gray (1867); Crié (1875); vi.1890, Herb. Fox Wilson, ⊕ (BM); Batters (1902); Lyle (1920); v.1930, Herb. Meinertzhagen, ⊕ (BM); Herb. E. G. Varenne, no date (SRD).

Unidentified geographical location: La Chaire, no other data (BM).

Les Ecréhous:

Chemin (1934*a*), 4.ix.1933, in large pools with sandy bottoms along channels between the rock masses at really low water.

The varied geological formations of the Channel Islands are neither particularly soft nor easily eroded; all the islands are essentially flat-topped eminences rising steeply from the submarine rock platform. Coastally, they are largely cliffed, with offshore rock reefs and platforms of varying but often gentle slope, considerable extent, and relative shelter from wave-action, especially along eastern-facing coasts.

Alderney:

The most generally exposed island to wave-action and fetch, Alderney has been rarely collected and observed; on both counts, it is therefore no surprise to find few records. The one specifically localised instance (Marquand) is from the more protected eastern shore, north side, where there are lower rocky masses containing pools.

Guernsey:

The southern and western coastlines are like those of Alderney, exposed to wave-action and

fetch from the west. Especially in the west, there are more sheltered sandy stretches abutting rocky platforms, in bays protected by headlands or other offshore reefs, than in Alderney. The north-west of the island, Cobo to L'Ancresse area, has the lowest rock/sand shores, providing records of *Padina*. The much larger number of records for Guernsey is not simply due to greater abundance. Guernsey has been a more generally visited island, by virtue of its larger size, easier accessibility, more accommodation, and greater variety of habitat. Marquand, who lived and worked in the Channel Islands, was responsible for the large majority of earlier original data from Guernsey.

Sark:

Rocks of Sark are all very resistant to marine erosion; the coasts remain steep and access is difficult. Phycologists have sufficiently frequently visited the island, so that the failure to record *Padina* must be due to the predominance of steep, very wave-beaten shores, with a general absence of detrital conditions over platforms in shallow standing water. Persistent examination of locally less wave-beaten sites would probably eventually detect plants.

Herm:

Few marine algae have been recorded from Herm; all *Padina* records date from the joint British–French Field Meeting, September 1960. Davy de Virville (1963 : 28–34) described the island, indicating that although the southern part is formed from granite and hornblende cliffs, the north is lower and sandy, with dune formations. Shell Beach, in the north-east, is about 700 m long; less directly wave-beaten than elsewhere, it is still affected by strong currents. The north of the west coast is relatively sheltered, with coarse sandy areas abutting sporadic rocky outcrops. Guernsey provides shelter from fetch, so that the effect of wave-action is not great. Shell Beach side, with coarse shell sand, shows a relatively poor flora, but at the south end, where it abuts on rocky areas, there are small pools with *Padina*.

Jersey:

This, the largest island of the group, is even more exploited for vacation purposes than Guernsey and has the longer history of phycological work. The earliest *Padina* records are mostly 30–40 years before those of Guernsey. All Jersey coastlines but the north have vast tracts of sandy beach uncovered at lower waters; even on the north coast, which is steep and forbidding, there are some small sandy areas. Amongst the larger tracts, St Ouen's Bay, Grève d'Azette, and St Clements Bay possess considerable areas of relatively low rocky platforms and reefs that abut or emerge through the sand, providing classical habitat conditions for *Padina*. The smaller sandy locations on the north coast also involve characteristic sand/rock transition areas; amongst these, Grève de Lecq actually has mid-19th century records of *Padina*.

Les Ecréhous and similar rocky groups in the Golfe Anglo-Normand:

Many such groups (e.g. les Casquets; Jethou; Brechou; les Ecréhous; les Minquiers; Îles Chausey; Grand Léjon; Barnouic; Roches Douvres; and les Dirouilles) exist in the Golfe. No records of *Padina* exist for most of these, probably due to a lack of sufficiently long-term or frequent collecting visits, although some smaller rock groups undoubtedly lack the required habitat conditions. Îles Chausey, for which there are many records, have already been dealt with (see Manche); only for les Ecréhous, of the remainder, are there published records. Les Ecréhous is a rock group midway between the north-eastern point of Jersey and the Manche shores at Cap de Carteret. Les Minquiers, Grand Léjon, Roches Douvres, Jethou, Brechou, and les Casquets, at least, have been visited by phycologists (Fischer-Piette, 1932; Davy de Virville, 1963) without *Padina* being recorded. Few *Padina* records from the Channel Islands are dated to day and month. Those that are show the same bias towards [July], August, and September as is general for northern areas within the *P. pavonica* range. Davy de Virville (1963 : 56), in a brief summary of the relationship of the Channel Island marine flora with that of the adjacent French coasts, stated: '. . . des espèces a affinité méridionale, comme *Padina Pavonia*, y sont plus rares'.

Ille-et-Vilaine

Rothéneuf:

Pointe de la Varde (Chemin, 1935), vii/viii,1934. Low water, on sandy bottoms between large rocks, with *Taonia atomaria*.

St Malo:

St Malo, Strand, 12.vii.1929, L. D. Brongersma and G. Sanders, 937.155.85 (L); Hamel & Lami (1930), common, vi–x, pools near Fort National, upper zone; Hamel (1939); Cardinal (1964), 6.viii.1963 and 24.ix.1963, J. Gaillard; De Brébisson, 910.161.585 (L).

St Malo and La Rance:

Hamel (1928), pools in basins with muddy sand bottoms, in calm inlets, summer, at *Fucus spiralis/F. vesiculosus* level.

St Servan:

viii.1873, Herb. Batters, probably juvenile, ⊕.

Area of Dinard–St Enogat:

Grande Vidé, before St Enogat: [a few km from the Laboratoire Maritime, Dinard]. Chalaud (1946), vi to ix, sandy locations, near large pool bordering drainage dyke.

St Enogat & St Suliac: Hamel & Lami (1930), hollows in median to upper zones.

St Enogat: Lami (1931), despite cold summer (1931) with poor light, *Padina* was abundant and well developed in hollows at upper level; Lami (1941), western end of couloir has a shallow and well-lit pool, warming up enough for *Padina*, viii.1940; C. den Hartog, 26.vii.1954, no. 1995, 956.266.278 (L).

Dinard: vi.1952, D. A. Hopwood (BM); 10.ix.1960, Pointe de Roche Pelée, J. Koster, no. 6926, 960.318.169 (L); Cardinal (1964), 6.viii.1963 and 24.ix.1963, J. Gaillard; Lestang-Laisné & Quillet (1972), ix.1965, high level hollows.

St Enogat plage, at Dinard, and Pointe du Décollé, at St Lunaire: Citharel & Villeret (1964), upper pools and rocks, 18.vi.1961.

Lefeuvre (1973) recognised three major coastal areas of Ille-et-Vilaine: (a) the Rance estuary, including Dinard to Rothéneuf, in which urban development (Dinard; St Servan; St Malo; Paramé; Rothéneuf) is the most important feature; (b) the median part, between Rothéneuf harbour and Port-mer-Cancale, comprising about 7 km of rocky and sandy coast that has largely escaped the extensive building of the western part; and (c) the eastern part, Baie de Mont-Saint-Michel, biologically an exceptionally rich bay and estuary.

There are reasonable numbers of *Padina* records, virtually all from the Dinard-Rothéneuf area. All were from the months [vi to] vii to ix [to x]; most are of relatively, but not very, recent origin (pre-1965). The later omission represents failure of observation, not absence. The concentration of records to the Dinard-Rothéneuf area is probably due to a balance of real differences in physical environment and the existence of the Laboratoire Maritime in the St Servan/Dinard area since soon after the First World War. The Pointe de la Varde, Rothéneuf, record of *Padina* (Chemin, 1935) seems to be the furthest removed from the Laboratoire. Further west, the shores are such that *Padina* is highly likely to appear, at least as ephemeral populations in favourable locations.

Côtes du Nord

Île Bréhat:

Beauchamp & Lami (1921), well developed on the eastern side of a hollow, in the sandy parts of small crevices.

Locquémeau:
Beauchamp (1914*b*), in shallow slightly sandy pools; Feldmann (1954), '. . . species aestival . . .'.

The scarcity of *Padina* reports in Côtes du Nord probably results from the few published algal surveys. The coastline does not present a wholly adverse physical environment and there are numerous locations of similar substrate and configuration as elsewhere support *P. pavonica*. Known records are unequivocal, and the situation is therefore not like that of the Cornish coast.

Finistère
Plage de Portez (*Conquet*):
Chalon (1905), Langeron.

Brest (*incl. Le Minou & Bertheaume*):
Crouan frères (1852), no. 76; (1867), in rock pools exposed to sun and freshwater influence, uncovered every day, Le Minou, Bertheaume, Douarnenez, summer; Stenfort (1877), on stones in shallow insolated pools with strong freshwater inflow, summer–autumn, rather common; 19.ix. 1880, C. Thiébaut, Baie de Bertheaume (Goulet de Brest), Herb. Société Dauphinoise, no. 3161, ⊕ (K in BM); Chalon (1905); *Hamel* (1939), Crouan fr., 1852; Baray in Herb. E. J. A. Gadeceau, probably juvenile, ⊕ (BM).

Banc de St Marc (*Rade de Brest*):
Wuitner (1921, 1946).

Lagonna–Daoulas:
Wuitner (1921, 1946).

Camaret:
Chalon (1905); 18.vii.1954, Conway, Presqu'île de Crozon (GL).

Morgat:
Wuitner (1921, 1946); 2.vii.1953, van den Hoek, no. 1837, 956.266.253 (L); 18.vii.1954, A. J. Davey, A2018, A2035 (UCNW); 18.vii.1954, van den Hoek, no. 1867, 956.266.261 (L).

Douarnenez:
Crouan frères (1852), no. 76; (1867), see under Brest, above; Chalon (1905), Crouan fr.

Audierne:
20.vi.1954, Audierne en St Perkus, J. Viergever, 'op. rotsen groeiend', 954.310.106 (L).

Below Plouhinec, coast about 2 km east of Audierne:
Prenant (1939), occasional at low water level amongst vegetation, on rocks, on very flat sand-covered granite.

Loctudy:
16.vi.1953, no. 650, van den Hoek, *F.*[*ucus*] *spiralis* level pool, 15 cm deep, SW aspect, in sand, 954.017.195 and 955.304.362 (L).

Concarneau:
Chemin (1927), somewhat widespread in hollows (pools), ix.1925.

Îles de Glénans:
Bouxin & Dizerbo (1971).

Portolonec:

2.viii.1882, Baray in Herb. E. J. A. Gadeceau (BM).

General:

Cove of Dinan (Kerloc'h) to Morne de Tréboul, via Cap de la Chèvre, Presqu'île de Crozon: Dizerbo (1946), in *Cystoseira/Laminaria saccharina* pools at *Fucus serratus* level . . ., can develop ahead of time, at beginning March, in good spring with favourable temperatures . . . a principal species of summer and autumn in sandy places, observations 1935–1941.

Baie de Douarnenez and Presqu'île de Crozon, between Camaret and Douarnenez: Dizerbo & Tourseiller (1959), rare on open coasts, common in the bay.

L'Île Cordinet [*Douarnenez–Tréboul region*]: Prenant (1939), on stones and sand, causeway island/mainland at very low tide, occasional, amongst the dominant *Laminaria saccharina*.

Finistère: Roemer in Herb. R. J. Shuttleworth (BM).

Brittany: Lyle (1923).

Padina shows patchy but locally abundant distribution in Brittany; it is symptomatic of this that the alga has rarely been reported from Roscoff. Cardinal (1964 : 60) indicated its absence from that area. This lack of records is unlikely to represent absence of observations or collections. Since the establishment of the Laboratoire de Roscoff in 1872, the immediate area has been subject to careful scrutiny over all seasons for many years. Chalon, the first director of the extended Roscoff Laboratory, published (1909) a list of the marine algae which had to that time been collected in the area around, including records by Crouan frères (1852, 1867), by himself earlier (1905), and some previously unpublished. Some apparent absences were sufficiently surprising for him to comment – '. . . Il faudra essayer en des places convenablement choisies des rochers, certaines naturalisations, telles que *Padina pavonia* . . . si abondants à peu de distance en conditions identiques . . .'. Chalon later published (1910) additions to his Roscoff list, noting *Padina* as present on not entirely satisfactory evidence '. . . D'après l'herbier du Dr. Denis . . .'. Among later workers, Beauchamp (1914*b*) indicated that *P. pavonica* doubtless grew towards the limits of the region, but he had no firm evidence of it elsewhere than to the east, at Locquémeau (Côtes du Nord), in flat sandy hollows.

Locquémeau is in a fairly sheltered position, but so are many other areas near it and apparently lacking, or not having reports of, *Padina*. This is equally true of the northern (English Channel) coast of Brittany, along which many localities have apparently the environmental conditions for supporting populations but for which no published data have been traced. As for Cornwall (*q.v.*), this is anomalous and can be confirmed or revised only by prolonged local studies. Apart from Holmes's Boscastle report, Cornwall equally lacks records from its north-facing (non-English Channel) coasts, whereas the south-facing (non-English Channel) coast of Finistère south of Îles d'Ouessant is rich in sheltered localities with abundant data on presence and distribution of *Padina*. For these latter records, patterns of distribution, habitat conditions, and maximum abundance/luxuriance periods agree with those noted elsewhere along English Channel coasts. Dizerbo commented (1946) interestingly on early (March) appearance of *Padina* in favourable years; this is consistent with events in southern England.

Morbihan

Gavres (*point south of l'Orient*):

Hamel (1939) (Montagne).

Quiberon Peninsula:

Davy de Virville (1952*a*), sheltered gentle slopes, in rocky *Cystoseira* pools amongst *Ascophyllum*, not common; Davy de Virville (1962), (i) on semi-exposed southern end of peninsula, from Beg er Lan to Pointe du Conguel, in pools below *F. spiralis*; (ii) Chenal du Trou, south coast before Pointe du Conguel, 27.viii.1949; (iii) in large channel with sand/mud bottom, at Goviro, near low tide level; (iv) on wave-beaten pebbly bottoms away from that channel; (v) similar channels at Port Goulvars; (vi) on flat rocks, at very low tide level, rocky Pointe du Canon (north

flank of Pointe du Conguel), on sheltered Baie de Quiberon coast of peninsula, tends to disappear end viii/beginning ix; (vii) sandy shores on sheltered Baie de Quiberon coast, on sand over rock and in *Cystoseira* pools amongst *Ascophyllum*; (viii) plage de Saint-Julien, 8.viii.1949.

St Gildas de Rhuys (*Presqu'île de Rhuis*):
Lyle, 22.vii.1926 (BM).

Belle-Île:
Wuitner (1931), in pools with runnels of freshwater, on schistose rocks, cove near Port Fouguet, ix.1923; hollows of Gros Rocher, ix.1928; *Hamel* (1939) (Gilgencrantz).

Morbihan:
Hamel (1939), Lloyd, *Alg. Ouest*, no. 155.

Although this southern root is much like the rest of Brittany, some of its east-facing shores are much more sheltered from the effects of long Atlantic fetch. *Padina* is well known from here, but for rather few places (principally Belle-Île-en-Mer and Quiberon); these largely represent areas examined, rather than realities of *Padina* distribution. Habitats in which *Padina* has been detected here differ little from those further north. It can reasonably be suggested that, anywhere in Morbihan, habitats of the type described by Davy de Virville (1952*a*, 1962) are likely at least periodically to support populations. Seasonality is not clear from published information; collecting periodicity of phycologists appears to be the major constraint on available data. The earliest traced collection date is late July (Lyle), although the Belle-Île and Quiberon data were gathered in August and September. The phenology probably differs little from that elsewhere in this northern part of the range, with an annual appearance in spring or early summer and degeneration of upright fronds during September or October, save in exceptional years.

Loire Atlantique; Vendée; Charente Maritime
Mainland coasts:
Le Croisic: Debray (1883*a*), Port and Jetty of Croisic, Grande Côte, 15.vii to 15.viii; Flahault (1889), pools in bay about lower neaps level; Cazal (1928), ix.1920, lower shore, on rocks; *Hamel* (1939) (Gomont); Lecocq (1975), trips with students, including May 1975.
Sion and Corniche Vendéenne: Lancelot (1961), on rocky facies at the foot of the Corniche Vendéenne, from before Sion and Croix-de-Vie to Pointe de Grosse-Terre, midlittoral, in hollows and channels, somewhat rare.
La Pironière: Lancelot (1961), rather common.
La Rochelle: *Hamel* (1939) (D'Orbigny).
Charente Maritime general: D'Orbigny (1820), common, coasts of Gulf of Gascony, particularly of Charente Maritime, level 2 (1·5 m below MHW to 4·5 m below MLW).
Note: if Hamel (1939) was reporting the La Rochelle record on the basis of specimen or MS data of D'Orbigny, this 1820 entry may also reasonably be reported as from La Rochelle.

Island coasts:
Île de Noirmoutier: *Hamel* (1939) (Brongniart).
Western coasts: Lancelot (1961), common on the gently sloping Rochers de la Loire, in front of Pointe de la Loire, midlittoral, in pools.
North-western tip: Lancelot (1961), Pointe de l'Herbaudière, rather common.
Northern coasts: Lancelot (1961), gently sloping rocky coast before Pointe de la Gardette, consists of small 'tables', at LW, whose irregular surfaces are separated by shallow channels and sandy-bottomed hollows below *Fucus serratus*, also occurs in *Rhodymenia* [*Palmaria*] band in June–July.
Île d' Yeu: Beauchamp (1923), in pools with gravel bottoms, mixed with [*Zostera*] meadows, in rocky facies.

North-eastern (landward-facing) coast: Lancelot (1961), from Pointe de la Conche to Pointe de Gilberge occur rocks, bordering the littoral and surrounding small beaches in sheltered circumstances, with *Padina*; also recorded at Ker-Chalon, Port-Joinville (common), and Anse de Broches (rather common).

South-western (ocean-facing) coast: Lancelot (1961), Anse du [Vieux–] Château, common.

Île de Ré: Beauchamp (1921), south coast, from Pointe des Baleines to Pointe de Chanchardon, wide sheltered intertidal with *Padina* in very flat hollows formed from the junction of rock layers; Beauchamp (1923), (i) in rocky facies, pools between the higher fucoids, (ii) non-rocky facies, in meadows and mussel beds, just north of Baleines lighthouse, west end of the island, with rich *Padina* in large *F. vesiculosus*-level pool, less well-developed population grows just to east of entry to Fier d'Ars, mid-north shore; *Hamel* (1939) (Lami).

North-eastern (landward-facing) coast: Lancelot (1961), common along the corridor-traversed rocky foreshore at Pointe du Lizay and along Côte des Portes, in flat pools on the rocky platform.

North-western point: Lancelot (1961), common in littoral pools on the long, wide rocky platform below the sands at the Pointe des Baleines, most wave-beaten point of the island, spring, summer, autumn.

South-western (seaward-facing) coast: Lancelot (1961), large plants common along walls of fish-ponds in slight sand deposit away from outflow points, rocky shore at Pointe de Chanchardon, near southern tip of island, between villages of La Noue and Sainte-Marie.

Île d'Oléron:

South-western (seaward-facing) coast: Lancelot (1961), Pointe de Chassiron, Domino, La Cotinière, rather common.

Lancelot (1961) described the physical environment of the whole area, including islands, between the estuaries of the Loire and the Gironde. He recognised (i) a northern (crystalline) rocky coast that terminates in the south at the outfall of the Mine, near St-Jean-des-Orbetières; sandy and muddy deposits occur, mainly in the bay between Île de Noirmoutier and Pornic, and at intervals between St-Jean-de-Monte and St-Jean-des-Orbetières; (ii) a southern (calcareous) rocky coast, more eroded than area (i), but with many detrital areas abutting rocky shores; (iii) the inshore islands of Noirmoutier, Ré, and Oléron, with general shore environment similar to the nearby mainland; and (iv) Île d'Yeu, further from the mainland, which has its own special coastal characteristics. Few of the *Padina* data derive from the mainland; the usual fascination for islands has resulted in the alga being best known on Noirmoutier, Yeu, Ré, and Oléron. Although elsewhere (in Morbihan and Finistère) records of *Padina* exist from similar environments to those along Loire Atlantique, in the latter Le Croisic is the only locality for which data are available. Published records from Le Croisic (1883–1975) are clearly all primary; they derive mainly from visits by phycologists to the Laboratoire de Biologie Marine du Croisic, which functioned over many years. On *Padina*, they are rather cryptic, only Flahault (1889) giving even an idea of the habitat. No real idea of phenology can be gained from the few records, since the collections probably again reflect phycologists' periodicity, not that of the algae. The collection dates suggest similarity to the phenology on adjacent shores to the north. No conclusion is possible on the basis of the even fewer mainland records from Vendée and Charente Maritime.

Lancelot (*op. cit.*) indicates that the eastward-facing island coasts are generally more sheltered than the westward-facing; the latter are at least exposed, in the case of the north-western tips very exposed, to strong wave-action. Clearly there is a range of different exposures along both sheltered and exposed coasts, depending on local and overall aspects; Lancelot considers that in detail. Although exceptions exist, the main rocky outcrops and platforms on all the islands are on the northern- and western-facing coasts, which probably explains why *Padina* records derive mostly from the exposed rocky shores, in shelter of pools, rather than from more sheltered eastern coasts. The cases (Île d' Yeu; Île de Ré) where records exist for landward-facing shores both involve the northern stretches in unusually rocky conditions.

Gironde; Landes

Gironde:

Arcachon: Chantelat (1844), moderately common along the edges of the dock, at Chapelle d'Arcachon, June, July.

Muollo: Chantelat (1844), moderately common along the edges of the dock at Muollo, June, July.

Gironde general: D'Orbigny (1820), coasts of Gulf of Gascony (Gironde), level two (1·5 m below MHW to 4·5 m below HLW), common.

Landes:

D'Orbigny (1820), see Gironde above; Sauvageau (1897), fond du Golfe de Gascogne (and therefore Landes), annual plant only once found during winter, as very small tuft among *Cutleria*, by contrast frequent in summer.

These almost unbroken expanses of coastline run virtually due south from the Gironde estuary (le Verdon-sur-Mer), to the rocky areas of Basses Pyrenées (near Bayonne). Loosely described as Les Landes or Côte d'Argent, the whole region shows coastal homogeneity characterised by Dangeard (1961 : 5) as '... plages sableuses et monotones de la région landaise ...'. The only significant interruption is the Bassin d'Arcachon, the source of the only precisely localised original records from Gironde. According to Chantelat (1844), this large natural basin at that time supported fairly common populations of *Padina* in at least two locations. *Padina* periodicity here was summarised by Sauvageau (1897), for Arcachon and the 'Fond du Golfe de Gascogne' (including Landes). Even this far south, periodicity accords well with that in England, where in mild seasons *Padina* can occasionally be detected during winter; possibly this is because the sea, except in lagoons along the sandy shore, is not so warm in Landes as on the more sheltered coasts to the north. Detailed treatment of the physical environment is presented for southern Landes by Dulau (1967).

Basses Pyrénées

Chambre d'Amour:

Evans (1957), widespread growths; Renoux-Meunier (1965), Cap Saint-Martin, Biarritz, channels, constantly immersed save for low spring tides, between irregular blocks on the foreshore below cliffs provide records of otherwise unreported species for the area, including (around LWS) *Padina*.

Nord du Promontoire du Halde:

Lancelot (1963), around and below MTL on sandstone, with large hollows, in several sandy pools well exposed to warm sunshine, summer and autumn.

Biarritz:

Peytoureau (1885); Roemer in Herb. R. J. Shuttleworth, received 1877, '... Les roches ...' (BM).

Guéthary:

Peytoureau (1885); Sauvageau (1920), vii/viii.1895, 1896, and ix.1920; *Hamel* (1931) (Sauvageau vii, viii); *Hamel* (1939) (Sauvageau); 9.ix.1854, Herb. G. Thuret (K in BM).

Rocks to south of Guéthary:

Hoek & Donze (1967), rock pools.

St Jean-de-Luz:

Peytoureau (1885); Beauchamp (1907), and coast from Pointe de Biarritz, at Cap Figuier, to opposite bank of Bidassoa at Hendaye-Ville, tide-pools with sand/gravel/consolidated pebble

bottoms, in small hollows between raised boulder arms, especially below Socoa fort; *Hamel* (1939) (Bory); Evans (1957), widespread growths.

Basse Pyrénées, general:

D'Orbigny (1820), coasts of Gulf of Gascony (Basse Pyrénées), level two (1·5 m below MHW to 4·5 m below MLW), common; Sauvageau (1897), fond du Golfe de Gascogne (and therefore Basse Pyrénées), annual plant only once found in winter, as very small tuft among *Cutleria*, by contrast, frequent in summer; Feldmann & Lami (1941), in sheltered stations, on bottoms covered by mobile substrata, and in sunny, sandy-bottomed hollows, well-developed.

There is a long history of original data on *Padina* from the rocky coasts of this most southerly area of Atlantic France. The considerable ecological and phenological data, much greater than for adjacent parts of France and Spain, are unequalled in quantity or detail south to the coasts of Portugal and Atlantic southern Spain. The generalised location of the earliest records (D'Orbigny, 1820) to the Gulf of Gascony must be taken to include Basse Pyrénées; a precisely localised and dated record for only 30 or so years later is known and there may be many other specimens in French herbaria that would add to, but not materially alter, the picture. For example, there is probably an approximately contemporary Bory specimen in Paris, since Hamel (1939) quotes 'St. Jean-de-Luz (Bory)', signifying a specimen seen. Sauvageau's (1897) general statement for the Gulf of Gascony (see Landes) also applies to Basse Pyrénées, being supported by Hamel's (1939) quotations from Sauvageau herbarium specimens and by precise data published elsewhere by Sauvageau (1920). Modern records (1940–70) indicate no significant recent change in the situation, on this coastline at least. Ecological details in modern work indicate the general requirement for standing wet conditions (best development in pools and channels); detrital conditions over rock; and (generally) strong insolation. On these coasts, there is good general agreement with the usual spring/summer/autumn sequence for the upright frond. Sauvageau's (1897) seems to be the only attempt to follow events during winter and early spring in this area.

Iberia

Northern Spain: Guipúzcoa to Pontevedra

Guipúzcoa:

D'Orbigny (1820), Gulf of Gascony (and therefore Guipúzcoa), level two (1·5 m below MHW to 4·5 m below MLW), common; Sauvageau (1897), fond du Golfe de Gascogne (and therefore Guipúzcoa), annual plant only once found during winter, as very small tuft among *Cutleria*, by contrast, frequent in summer.

Santander:

San Vicente de la Barquera: Sauvageau (1897); *Seoane-Camba* (1965).

Cabo Mayor: G. T. Boalch, 20.vii.1966.

Oviedo:

Gijon: Sauvageau (1897); Miranda (1931), area from outfall of La Ñora, east of Cabo de San Lorenzo, west to Cabo de Peñas, Ría de Avilés, and Playa de Xagó, frequent in pools, upper littoral, fruiting in summer; *Seoane-Camba* (1965).

Lugo:

Rivadeo [= *Ribadeo*]: Sauvageau (1897); *Seoane-Camba* (1965).

La Coruña:

Sauvageau (1897); *Seoane-Camba* (1965).

Pontevedra:

Bay of Vigo: Seoane-Camba (1958), amongst *Enteromorpha ramulosa*, in inlets.

Ría de Vigo: Lázaro (1889); Seoane-Camba (1957), abundant at Canido, Samil; Seoane-Camba (1960), *Padina/Cladostephus* communities in protected locations; *Seoane-Camba* (1965).

Very few records have been traced for northern Iberia, although local habitat conditions would appear frequently to be adequate. The sparse records reflect the general rarity of collections. There is no precisely localised information for Guipúzcoa and none at all for Vizcaya. Santander is also poorly recorded, but at least there are localised modern primary data; additional information possibly exists in the herbaria of Sauvageau, Miranda, and other phycologists who have collected along the north coast. Since the two original observations are nearly 70 years apart, comment on continuity of populations and on phenology is not possible. Oviedo shows the same pattern as Santander, except that its most recent original record (1931) is much older; it may be supported by material, but that has not been checked since Miranda was on the whole accurate in his statements. Lugo and La Coruña are recorded only in primary early statements by Sauvageau. Pontevedra, essentially the Ría de Vigo, has been recorded in original observations on a few occasions; apart from the early record by Lázaro, original floristic and ecological observations by Seoane-Camba, including characterisation of an association or subassociation, are important. *Padina* is widespread and abundant as a characterising element associated with *Enteromorpha ramulosa* and *Cladostephus verticillatus*, amongst others, in 'protected locations'. Surprisingly, the nearby and similar Ría de Arosa, Ría de Pontevedra, and La Guardia (Desembocadura del Miño) were not recorded as locations for *Padina* during work by Seoane-Camba (1957). The many records for Portugal and Atlantic southern Spain suggest that, for La Coruña and Pontevedra, *Padina* should not be difficult to detect in suitable ecological conditions.

The Ría de Vigo plants show aspects of similarity to *Padina* behaviour in the Mediterranean. A *Padina pavonica–Cladostephus verticillatus* association was described in the latter (Feldmann, 1937) along the western coast of Golfe du Lion, from Collioure to the Franco-Spanish border at Cap Cerbère. The habitat conditions for this synthetic association are horizontal rocks covered with sediment (sand or sand-mud), in shallow depths (MSL to 4–5 m deep) or in deep pools, in strongly insolated calm locations. Seoane-Camba and Feldmann were thus concerned with essentially the same ecological grouping in the same ecological conditions. On the south coast of England, *Padina* occurs in conditions closely similar to those described here (although not found even as deep as 5 m into the infralittoral); not uncommonly the alga also is found growing alongside *Cladostephus*, but that grouping is neither sufficiently consistent nor adequately characteristic of the flora in which it occurs to be termed an 'association', at least in our experience. According to Ardré (1971), the lower horizon of the littoral and the infralittoral in moderate exposure or shelter along the southern Portuguese coast is similar; 'particularly common' species listed included both *Padina pavonica* and *Cladostephus verticillatus*, neither more particularly characteristic of the flora in these conditions than any other species in the list.

Portugal

Douro Litoral:

Foz do Douro: Hauck (1889); *Ardré* (1970).

Estremadura:

Sesimbra: Palminha (1951), Fundeadouro; Ginsburg-Ardré (1963); *Ardré* (1970), quoting Palminha; Ardré (1970), 26.vi.1961, 21.iv.1963, 5.x.1963.

[*Portinho Da*] *Arrábida*: Palminha (1958); *Ardré* (1970); Ardré (1970), 22.iv.1963.

Near Cetobrigam [? *Setúbal*]: Welwitsch, F., *Phycotheca lusitanica*, no. 149, $18\frac{42}{50}$ (BM).

Tróia, near Setúbal: Rodrigues (1963), citing Welwitsch, s/n, iii/1850 (in COI and LISU, P46430); s/n, iii–iv.1850, in LISU, P46432; Ardré (1970), citing P46432, cf. last entry.

Setúbal: Henriques (1881); Rodrigues (1963) and Ardré (1970), both citing Lami, s/n, x.1932 (COI); *Ardré* (1970).

Baixo Alentejo:

Sines: Ginsburg-Ardré (1963); *Ardré* (1970); Ardré (1970), 1–2/vii/1961, 4.x.1963.

Vila Nova de Milfontes: Dizerbo (1954); Rodrigues (1963) and Ardré (1970) both citing Welwitsch, s/n, iv.1848 (LISU P46430, P46433); *Ardré* (1970).

Algarve:

Sagres: Ginsburg-Ardré (1963); *Ardré* (1970); Ardré (1970), 27.ii.1960.

Praia Da Rocha: Palminha, no data; *Ardré* (1970); Ardré (1970), 25.ii.1960, 1.x.1963.

Praia Do Carvoeiro: Palminha, no data; Ginsburg-Ardré (1963); *Ardré* (1970); Ardré (1970), 15.viii.1960 and (J. Feldmann), 2.x.1963.

Ria De Faro: Palminha, no data; *Ardré* (1970).

Doubtful location: *Torgulho*: Herb. R. J. Shuttleworth, rocks, vi.1837 (BM). [Possibly a location near Almada, south side of the Tejo (Tagus), north of Sesimbra; hence, Estremadura.]

Portugal general: Rodrigues (1963), aestival in Atlantic, iv to x; Ardré (1970, 1971), moderately wave-beaten to sheltered shores, base of lower littoral and in infralittoral, on rocks covered by sandy sediments, often in very well lit positions.

Relatively well worked for some time, Portugal has recently been subjected to detailed long-term study by Ardré (1970, 1971). Some *Padina* populations there are of considerable longevity, e.g. that at Vila Nova de Milfontes, sampled by Welwitsch (specimens dated 1848) and Dizerbo (1954), and noted by Rodrigues (1963) and Ardré (1970). There is indication that seasonal periodicity is now beginning to show rather less consistency than further north; many more collections of erect fronds date from earlier (February to April) and later (October) than is the case for English and French populations. Ardré's (1971) information indicates no real difference in habitat requirements between British and Portuguese populations. Both demand shelter from direct strong wave action, although consistently wet conditions (usually standing water) are necessary; both appear in the lower littoral and shallow infralittoral, on rocks covered with detritus.

Evenly spread geographically, the available data are not sufficiently extensive for certain recognition of *Padina* distribution foci along the Portuguese coast. However, except for the single record from Douro Litoral, all the available information derives from the southernmost coastal provincias, Estremadura, Baixo Alentejo, and Algarve. Ardré's recent work was sufficiently detailed and geographically widespread to demonstrate that this was not merely a matter of chance distribution of collections, but had some real meaning in terms of *Padina* biogeography in Portugal. Given tolerable local environment, *Padina* clearly grows better the further south it occurs along Atlantic shores, towards the Mediterranean. The absence of records from the eastern half of Algarve, beyond Faro, and from the whole of Huelva (see Atlantic southern Spain) is probably to be explained by lack of adequate firm, detritus-covered substrata; both regions are very swampy and sandy.

Atlantic southern Spain: Huelva and Cadíz

Huelva:

No data traced; see note to Portugal.

Cadíz:

Chipiona: Seoane-Camba (1965), viii, on rocky platform, somewhat covered by sand and mud.

La Caleta (*Cadíz*): Seoane-Camba (1965), vii, small specimens towards low water.

Cadíz: *Plantas de Andalucia*, 1803, Leblech & Roxas Clemente, no. 313, 'Variedad de *312*' [young *P. pavonica*], no. 312 (MS Clemente) [older *P. pavonica*], on rocks by the castle of Sn. Sebastian in Cadíz, mid-April, most abundant, Herb. R. J. Shuttleworth (BM); 161, most abundant on rocks by the castle of San Sebastian in Cadíz, 29.iv (MS Clemente) (K in BM); prope Gades, Dunze, 1803, Mertens, Roemer in Herb. R. J. Shuttleworth (BM); Clemente (1807) (as *Fucus pavonius* L.); Seoane-Camba (1965), stn 79; specimens with no other data (two very young, one older) (K in BM).

Between Cadíz and Torregorda: Seoane-Camba (1965), stn 86, ix, pools.
Torregorda: Seoane-Camba (1965), stn 90, x.1959, rocks to the east, in protected pools.
Conil: Seoane-Camba (1965), stns 109/110/111, iv.1959, north of Conil.
Cabo Trafalgar: Seoane-Camba (1965), stns 128/130/131, near the Cabo, v.1959.
Playa de la Victoria: Seoane-Camba (1965), vii.1960.
Barbate: Seoane-Camba (1965), drift on shore, vi and viii.
Tarifa: Clemente (1807); Seoane-Camba (1965), stns 178 (near Tarifa) and 181 (south of Tarifa), iii to ix, always in somewhat protected sandy locations.
Punto Carnero: Seoane-Camba (1965), xii.1959.
Algeciras: Clemente (1807); Seoane-Camba (1965), stns 193 (north of Algeciras), 203, and 204.

General circumstances of *Padina* in southern Spain obviously represent a transition from the Atlantic coast into the Mediterranean, but it is convenient here to terminate detailed consideration of data at the eastern boundary of Cadíz. The relationship between characteristics of Atlantic and those of Mediterranean populations is discussed elsewhere. Only records from Huelva and Cadíz are considered here; functionally, that means Cadíz alone, since no information has been traced for the northern part of the Golfo de Cadíz. The reason for this may be the sandy and swampy nature of that coastline, in large part known as 'Arenas Górdas' (=coarse sands). The area is strongly affected by outfall from various large freshwater systems, including the Guadiana River (the Spain–Portugal coastal boundary); the Canales (Channels) that outfall near Huelva; and the Guadalquivir. A coastline like this, largely lacking rocky substrata, is rarely attractive to phycologists. Cadíz, by contrast, has considerable information, some as early as 1803. The most detailed data derive from Seoane-Camba's (1965) study of the Cadíz littoral; he examined many stations over the whole area from Sanlúcar de Barrameda (the Guadalquivir mouth) in the north, round to Algeciras in the east. *Padina* was present wherever habitat conditions permitted. Populations are possibly also present here in the shallow infralittoral; Seoane-Camba's data represented primarily intertidal and infralittoral fringe collections. Habitat demanded resembled that in areas further north; that is, pools and wet conditions, on rocks covered by sand or detritus, principally around low water and with some protection from direct wave-action. Some populations were of considerable longevity; as with the distribution foci in England, the immediate area had clearly borne *Padina* for many years, even though precise identification of consistent individual populations was not possible. Specimens identifiable with Clemente and with Mertens, from Cadíz or nearby, date from 1803, and Seoane-Camba recorded the alga from there in the years to 1965; the 1803 specimens undoubtedly formed the basis for Clemente's (1807) published record from Cadíz. He also recorded plants from Tarifa and Algeciras, both of which still carried populations in 1959–60.

The available data again provide some support for further breakdown of the seasonal periodicity generally found further north. Seoane-Camba (1965) recorded the alga from some stations in March and April, and Clemente's (1803) Cadíz material appears to have been collected in April. At Punto Carnero, Seoane-Camba noted *Padina* in December (1959), demonstrating further merging into the situation outlined (Feldmann, 1937, and others) for the western Mediterranean, where *Padina* is detectable as upright fronds over virtually the whole year. Surprisingly, Seoane-Camba makes no mention for Cadíz of the association characterized by *Padina* and *Cladostephus* that he recorded widely for the Ría de Vigo, northern Spain; a very similar association had earlier been recorded by Feldmann (1937), among others, from Côte des Albères, on the Mediterranean Spanish–French border.

Discussion

Trends in distribution

This critical assessment of all traced data demonstrates so far as is possible the past and current trends in distribution of *Padina pavonica* in the area covered. Many of the available signs indicate the occurrence in comparatively recent times of quite profound changes toward the periphery of

the distribution in the British Isles and, perhaps, in adjacent areas. At least on British shores, the changes seem largely to have involved peripheral withdrawal, which a comparison between past authenticated reports and present detailed observations clearly indicates. By contrast, in Dorset a local tendency to the opposite effect has been suggested by Burrows (see Dorset: Kimmeridge Bay). Evidence for this as a general tendency is slight and any detected expansion may remain both local and ephemeral.

Changes such as these are neither easy to predict nor simple to elucidate, even though the British coasts clearly represent part of the northern distributional limits of the species. An increase in environmental pollution may be a factor contributory to the local changes in some areas, but it is not likely to be the principal overall reason. Long-term natural fluctuations or other major events both within and outside the alga need to be examined in critical detail. This is not often possible; there is a lack of biological data on many aspects of the species. Where there is evidence sufficient to indicate possible influence on the distribution, the effects have been examined. Harvey (1849 : pl. 91) indicated *Padina pavonica* to be '. . .[1] abundant in the Tropical Ocean, and reaching its northern limit on the southern shores of England, without exhibiting any depauperation from climate. The British specimens are fully as large as those from warmer latitudes, and as well coloured. [2] This being the case, one would naturally expect that it may yet be discovered further north . . .'. Comments [1] and [2] bear on biological events and on distribution, and are worth examining in the light of all available data: [1]. The majority of specimens from the Mediterranean infralittoral appear to be of greater size than most British plants, although there are exceptions (see Dorset: Chapman's Pool). Liddle (1975) has shown that *P. sanctae-crucis* (correctly *P. jamaicensis* (Collins) Papenf.) responds to the stress of growth in the intertidal by comparable reproductive maturity and activity at a size on average smaller than plants in the analogous state in the subtidal. Since reduction in size does not necessarily, except in its extreme, reflect depauperation, Harvey's remarks are to that extent correct. [2]. Individual northerly reports are considered under counties. As to the more general pattern, it is not clear if the peripheral distribution in northern Europe is due to past and current changes that are phasic, or to entirely random or irregular variations in populations from time to time. If the pattern includes advance and retreat components, regular or irregular, of distributional change, the available data reliably demonstrate for recorded time only the retreat component outside the foci of distribution, although within the latter at population level both components may be occurring contemporaneously in different locations. At the level of overall British distribution, available information therefore suggests that gross loss and gain changes normally require very long periods of time to be fully effective, although locally adverse conditions may rapidly affect the distribution of populations. There is certainly no evidence of both loss and reappearance in any of the areas peripheral to the foci, most of the facts pointing to loss and just a few, such as the Cork Harbour find, to recent ephemeral gain. Very long periods of observation would be necessary to establish the overall nature of the pattern with certainty; some such observations are in progress by one of us (W. D. R.). The shores to commence with are clearly those for which previous authentic records exist in the absence of current populations. The best summary of the revealed overall pattern is that the British, French Channel, Belgian and, Dutch coasts form an area of which the marine environment is in places (the warmer, shallow water 'cases') tolerable to *Padina* from time to time. Since the alga as now known is quite specific in its habitat requirements, only areas away from the direct effects of strong wave-action are ever likely to support populations.

Origins of populations and distribution foci

Speculation on the origin of *Padina* populations and distribution foci on southern British shores really requires more information. The outlined contraction in distribution could be taken to indicate that the present areas with long histories of records (Devon; Dorset; Isle of Wight) are simply relict foci of a distribution previously much more widespread on all parts of the coasts of the British Isles. In view of recent work on the sea-surface temperatures of the Ice-Age earth (McIntyre *et al.*, 1976; Lamb, 1977), this seems rather unlikely. If the present distribution results from gradual and fluctuating progressive spread into Britain from the south at some time in the

historically distant past, then the sites of primary introduction seem likely to have been in Dorset or Devon, from the favourable ambient conditions and the size and vigour of populations and individuals there. Certainly the east Devon focal area of *Padina* possesses by far the longest history of being recorded in publications, although specific populations there may have fluctuated widely within particular locations. The available evidence does not permit meaningful comment on the time scales involved in any changes.

Reproductive patterns

Demonstrably, Dorset, east Devon, and the Isle of Wight form the main foci of the present distribution pattern, and all these have firm, long- and well-established *tetrasporangial and vegetatively perennating populations*. Suitable areas peripheral to and/or within the foci carry some populations, generally small, that are ephemeral and appear and disappear over variable periods, perhaps as a result of the isolated or combined effects of changes in configuration or substrata on shore; of temperature variations (see Ayr); of the effects of population size or population vigour; or of similar phenomena. The coincidence of tolerable environmental conditions with an adequate concentration of viable spores seems likely by chance to be a rare event, especially in areas outside any of the well-established foci at the periphery of the general distribution range. Near that periphery of its distribution, the specific habitat requirements of *Padina pavonica* are more rarely satisfied by less abundantly available tolerable conditions present over a lesser vertical amplitude than in the major centres. The alga thus shows signs of even greater dependence on local vegetative perennation and spread than on spore formation. Observations by Norris (*op. cit.*) and in this paper indicate that those individuals or lobes of largest size and/or most maturely reproductive are generally found towards the centre of clumps of specimens; perennation through adverse conditions by rhizomatous portions has previously been discussed (see p. 4). Both these observations point to the importance of vegetative perennation and spread in British populations. Plants in the British foci of distribution are very rarely sexually (gametangial phase) reproductive and only restrictedly (July–October) tetrasporangial in large numbers; this would seem to place a limit on peripheral *new colonisation* by spore saturation except in the most favourable circumstances. *Recruitment* of spores within the distribution foci that exist, however, may be more effective.

At least at some times of the year (and it may be significant that it is in the months before the onset of the usually least favourable time of year for the erect alga) the extent of tetraspore development is locally adequate to supply whatever is required as periodic replenishment and re-invigoration for the otherwise largely vegetatively maintained populations. Depletion of the main vegetatively reproducing basis of the local population could possibly in this way be offset so that size (? numbers or density) and vigour do not usually fall below the level required for population maintenance. This postulated ideal is not always realised in practice, as population loss and gain within and without the focal areas of the south clearly demonstrates. The optimal balance, whatever that may locally be, between spore supply and vegetative vigour is by no means always achieved. The circumstances favourable to *new colonisation* do occasionally occur and can be effective; this is attested by the recent ephemeral find in southern Ireland. The same conclusion is suggested from what seem to be past variably ephemeral populations in Sussex, Kent and Essex, and perhaps in Cornwall, Lancashire, Ayr, and north and south Wales. The reports from Ayr and from comparable situations in Europe are not easy to accept as having been based on attached material.

The assessment of these populations as ephemeral is to a degree speculative. No importance has usually been attached to absence of data before the first record (except as indicated within county entries) nor, generally, to similar absence between records unless there has been traced comment or data showing unusual significance of the absence. 'Ephemeral' therefore indicates only that there are a few authenticable past records, variably spaced throughout time, from an area where plants cannot now be traced.

Validity of earlier data

It has been rightly remarked of *Padina* (Harvey, 1847) that on the whole '. . . it is difficult to imagine what could have been mistaken for it, so different in appearance is it from all other Algae'; even

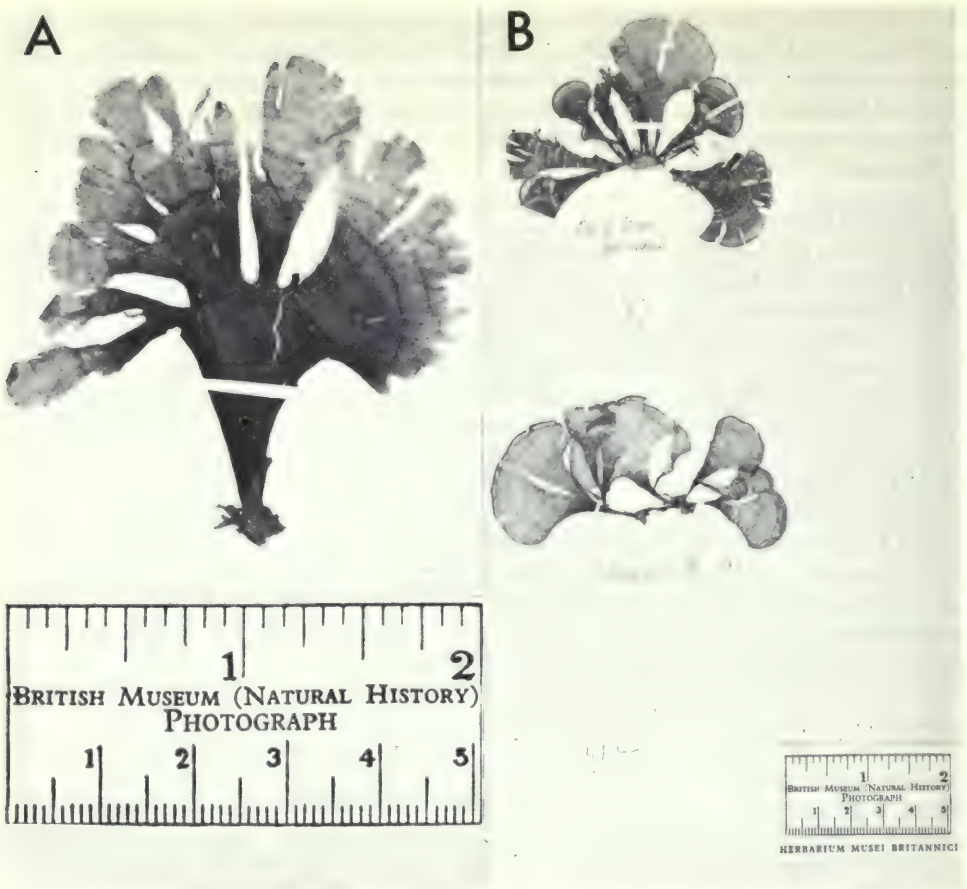


Plate 3 **A:** A *Padina*-like plant of *Taonia* from Brighton, collected by Mr Pike in 1854. The colour is more yellowish, the texture peripherally rather more delicate, and the apparent splits more pronounced, than is usually the case with *Padina*; similarly, the surface of the plant is neither roughened nor slightly whitened. However, on shore, it would be relatively easy for an inexperienced observer attempting quick determinations to confuse the two. Compare this with the correctly determined *Padina* in Plate 3B. Burnett Collection [BM]. **B:** Specimens of *Padina* from approximately the same era as the *Taonia* of Plate 3A. Note the close resemblance of the lower right and lower left plants on the upper (Isle of Wight; September 1860) clump of *Padina* to the plant of *Taonia* illustrated in Plate 3A. Burnett Collection [BM].

the above doubtful or unlikely populations or individuals are therefore difficult to dismiss without further consideration. There is only one real possibility of confusion in determination of *Padina* on British shores. Those with little field experience could find that distinguishing between *Padina* and *Taonia*, in some states, could raise problems. The rather flabelliform growth-form of *Taonia* that sometimes occurs amongst populations on even the south-eastern coasts of England (where *Taonia* occurs less frequently than is usual elsewhere) could be taken for degenerating specimens (with vertical splits) of *Padina pavonica* (see Plate 3, A & B). *Taonia*, although rather more tolerant of exposure to wave-action than appears generally to be true for *P. pavonica*, is still mostly present in similar conditions to the *Padina*, sometimes even alongside it. It is not easy to believe, however, that all those experienced workers indicated earlier, recording or discussing occurrence of *P. pavonica* in the most specific terms, could have made this mistake in observation.

Some of the available reports could have been derived from drift material, even when not so acknowledged. Despite our own observations on the rarity of *detached* drift material being thrown up on British shores, there are 18th and 19th century reports of drift specimens, attached to small stones, pebbles, or fragments of rock, thrown up on the shores, especially of Belgium and Netherlands but also in some parts of England (see Pulteney, 1799; Pulteney [& Rackett], 1813). Since most of these reports are more or less contemporary with the unusual British records examined here and both are often the only basis for subsequent acceptance of *Padina* in the local flora, there must be reservation as to the part played by drift. *Padina* populations may (although there is no evidence for it) have been then much larger in adjacent more favourable areas, giving rise to greater amounts of drift, detached or still attached to fragments. Seoane-Camba (1965), for example, has recently recorded drift material of *Padina* at Barbate (Cadíz), an area where many populations are known. It remains unlikely that drift material could be the explanation behind the observations made on British coasts by Hill (Sussex) or by Smith, Sowerby, & Johnson (Sussex; Kent), much less of the precise data recorded by Turner (about the Leathes Margate record), by Wood (Kent), or by Dale in Taylor and Dale (Essex).

Variations between Britain and the adjacent continent

The apparent general absence, with the poorly-authenticated exceptions indicated earlier, of *Padina* from Cornwall is curious and anomalous. The situation in Brittany, the French analogue of Cornwall as to position and marine physical environment, emphasises still further the strange absence from the far west Channel coasts. Distribution of *P. pavonica* in Brittany is by no means continuous along the coasts; in view of its moderately strict habitat requirements, the alga could not be expected to appear everywhere there. However, there are long stretches on the north coast (between Locquémeau and Conquet) where conditions are apparently suitable (e.g. as at Roscoff) but in which *Padina* is rarely if ever recorded. Generally elsewhere in Brittany, plants are locally and seasonally very evident. The whole county of Cornwall, by contrast, with many suitable areas of substrate, shelter from wave-action, and adequate temperature régime, seems now to lack populations with any longevity. We have no good modern evidence that even sporadic individual plants appear there. If they are confirmed by intensive surveys, these distributional blanks will re-emphasise the strong likelihood that breeding populations and established vegetative populations of some so far unknown minimum size are necessary if the alga is consistently to appear, even in otherwise suitable circumstances, towards the northern limits of its eastern Atlantic distribution.

There is an apparently strong resemblance between the general form of the distribution on British southern coasts and that on the northern French Atlantic coasts, the latter including the Channel Islands. Since there is considerable correspondence in substrata and their distribution on the two sides of the Channel, as well as similarities in other aspects of the physical environment, this is not surprising. The Channel coasts of France are not so much nearer to the present distribution centres of *Padina* that significant variations attributable to behavioural differences, environmentally or internally determined, are likely. 'Foci' in the *Padina* distribution pattern on French shores of the English Channel are therefore to be expected, of which the similarities in distribution on both sides of the Channel are principally a reflection.

There appear from available information to be no tremendous or sudden changes in the biological characteristics shown by *Padina pavonica* in the different areas and populations to be found between Brittany in the north and Cadíz in the south, although the general trends are not always absolutely maintained at local level. There is no apparent change in substrate or other habitat requirement along the whole north-east Atlantic coastline from Great Britain southward to Algeciras. Temperature and insolation with depths, and hence the overall depths within which the levels of these are tolerated by *Padina*, clearly vary between Britain (where there has never been an authenticable record deeper than the immediate metre depth of the infralittoral fringe level) and the Mediterranean (whence valid records from considerable depths have already been indicated earlier). Temperature is probably the principal constraint in this, although the sequence of change may be misrepresented due to lack of information. There could, for example, be plants in greater depth than so far recorded for the infralittoral along Atlantic mainland (e.g. Portuguese and southern Spanish) coasts. Further information is required on both this and the following points.

Periodicity of biological phenomena

Changes in the periodicity of biological phenomena such as presence of upright fronds and production of viable or inviable reproductive structures cannot yet be traced in detail along the whole length of the coastlines within the northern Atlantic/Mediterranean distribution of *Padina*. Certain areas of the Mediterranean, however, are known to yield sporangial plants over much more of the year than is normally true for Britain, and (see Introduction) within a few Mediterranean regions, populations at some depths quite commonly include high proportions of gametangial plants. To some extent, it *is* possible to begin tracing the changes in length and placement during the average year of the period when recognisable upright fronds of *Padina* can be detected, in contrast to the perennating basal parts of the alga. By the entrance to the western basin of the Mediterranean, upright fronds are more or less consistently present all the year round in the infralittoral, although Feldmann (1937) has indicated the probable involvement of overlapping generations in this. Atlantic areas north of and nearest to the Mediterranean (Portugal; Cadíz) not surprisingly show more of a tendency toward the Mediterranean periodicity than do areas further north. The differences are relatively slight, and the existence of a real trend cannot be confirmed without extended study of the situation at selected spots from Britain to the western Mediterranean. Chance differences in behaviour between the different years of observation *could* have led to recognition of trends more apparent than well-founded. In England, *Padina* has been shown to be present as upright fronds for longer periods, persisting well into the winter or appearing early in spring, in some years than in others. Reasons for these variations in phenomena are not fully understood, but more likely they concern environmental aspects to which the plants are responding than spontaneous variations within the alga itself, although both may be implicated. There seems to be relatively little real variation in time of appearance of upright fronds in any area between Britain and northern Portugal. Variations of this kind seem on present evidence to occur south of northern Portugal.

There is overall need for careful long-term scrutiny of all shores or local microniches actually or potentially capable of supporting *P. pavonica*, especially in southern Great Britain but also elsewhere in the island group and throughout adjacent continental shores. Particularly desirable is a more detailed search of suitable infralittoral areas in southern Britain and in the transitional N. Spain/Portugal/S. Spain area. It remains to be established whether the apparent rarity of gametangial material in all but a few Mediterranean locations is due to simple lack of adequate observations, to actual loss of potential, or to environmental constraints that are quickly reversible in isolation from the natural living conditions. In view of the demonstration (Edwards 1973, see Introduction) in a similar case in *Ceramium* that the potential is merely suppressed, being realised in very few individuals in the field but readily expressed in culture, additional field observations and culture studies on British south coast material of *Padina pavonica* would be of considerable biological interest. We would like to think that, when and if further studies on aspects of *Padina* in this area are carried out, this paper will provide an authentic basis against which distributional or biological variations can be assessed.

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Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. III. Rhodophyta (Bangiophyceae)

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Synopsis

This paper assembles and, so far as is possible without extended field and herbarium studies, examines critically the validity of records of marine and brackish-water Bangiophyceae for the western coast of tropical Africa. The whole mainland coastline from the northern boundary of former Spanish Sahara southwards to the southern boundary of Namibia [former South West Africa], the oceanic islands from the Salvage Islands southwards to Ascension, and all islands close to the African mainland coast are included in the area covered. Each species entry includes all traced records for the species, the names which have previously been applied to it for the area, and additional comments or evaluation, as necessary. Comments have also been made at generic level in certain difficult cases.

Introduction

The area dealt with in this part is the same as that covered by parts I (Lawson & Price, 1969) and II (Price *et al.*, 1978). A coastline map of west Africa (Fig. 1) provides details of names and boundaries of the constituent countries. The arrangement of genera and species is no longer presented as a single alphabetical order. This was possible in the previous parts because the coverage of each group was complete in the single part. With the greater numbers of Rhodophyta (red algae), complete coverage in one publication was not feasible and division by systematic arrangement at class, order or family level according to the size of the particular group has therefore been adopted. The present part (class Bangiophyceae) is arranged alphabetically in order of genera and species *within* the above hierarchy.

Each main species entry consists of three, sometimes four, principal parts:

(i) *The major bold heading*, which represents the accepted species name and authorities.

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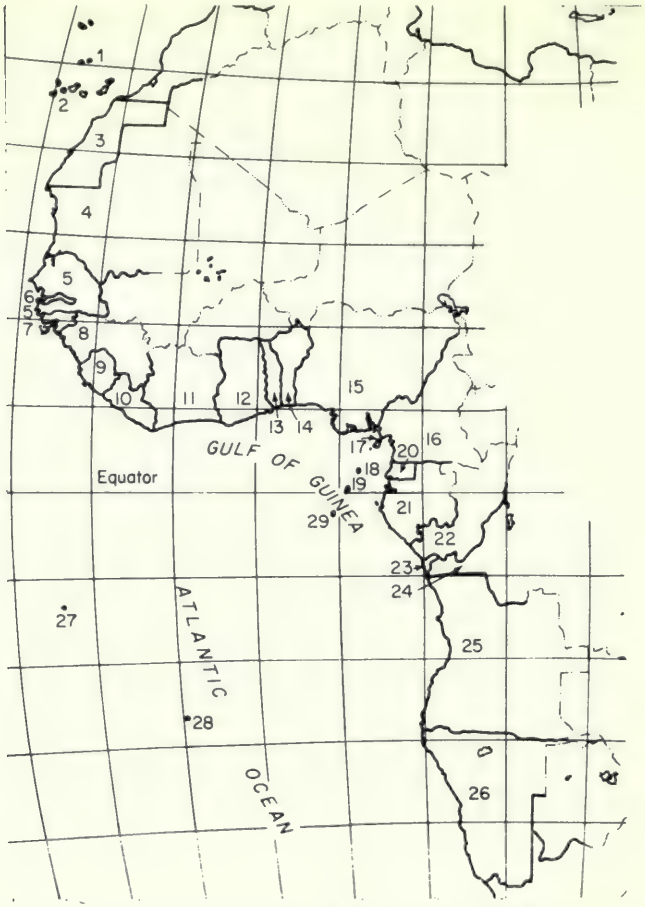

Fig. 1 The coastline of tropical west Africa and the offshore islands.
1, Salvage Islands: 2, Canary Islands; 3, * former Spanish Sahara [= Western Sahara, Spanish West Africa] (includes the often-quoted Rio de Oro, the southern region of the country, but excludes Ifni); 4, Mauritanie; 5, Sénégal; 6, Gambia; 7, Guinea-Bissau [= Portuguese Guinea]; 8, Guinée; 9, Sierra Leone; 10, Liberia; 11, Côte d'Ivoire; 12, Ghana; 13, Togo; 14, Benin [= Dahomey]; 15, Nigeria; 16, Cameroun; 17, † Macias Nguema Biyogo [= Fernando Póo]; 18, Príncipe; 19, São Tomé; 20, † Equatorial Guinea [= Spanish Guinea]; 21, Gabon; 22, ‡ Republic of the Congo; 23, Cabinda; 24, Zaire [= Congo Republic]; 25, Angola; 26, § Namibia [= South West Africa]; 27, Ascension Island; 28, Saint Helena; 29, Pagalu [= Annobon]. The Cape Verde Islands, which lie immediately to the west of Dakar (Sénégal), have been omitted from this map but are included in the species list.

* The former colony of Spanish Sahara no longer officially exists, the territory it once covered being divided, by agreement, between Morocco and Mauritanie. The effective date of the division, Spain concurring, was 28 February 1976, although guerilla opposition delayed matters until a formal agreement on 14 April 1976. The attempt to maintain the territory as the Democratic Saharan Arab Republic has apparently entered 'the realm of myth' (Gretton, 1976). The authors' citation terminology is maintained throughout the records.

† Nos 17 (Macias Nguema Biyogo) and 20 (Spanish Guinea, = Rio Muni) on the original map (Part I) are now jointly administered as Equatorial Guinea.

‡ Loango, a name much used by early collectors such as Welwitsch, was formerly a coastal region of west Africa. Its application appears to have included much of the coastline of the Republic of the Congo (22), as well as of Cabinda (23) and Zaire (24). Because by far the longest and rockiest part of the Loango coast lies now within the Republic of the Congo we have attributed all marine algal records from Loango to the Congo.

§ Namibia, previously the coastal strip only, is now applied as the official name of the whole country. Form of the original citation in published works is maintained in the list.

(ii) *Subsidiary italicized headings, in square brackets.* These represent the different ways in which the species has been cited by authors publishing records of relevance. The manner of citation by species names, even when manifestly incorrect, has been maintained unless the original author's intent required clarification for comprehension; there will thus be no doubt as to which record we attribute to which accepted species.

(iii) *The distributional data*, within which the countries are arranged in alphabetical order and more generalized statements of distribution appear after the specific countries. The latter statements are included *verbatim* as it is not always clear for precisely which countries they establish records. The numbers given in parentheses after each country name or generalized statement of distribution refer to the corresponding numbers in the references. Works cited in the present list of Bangiophyceae have been newly numbered so that a given number here does not, except by accident, correspond to that given to the same reference in previous parts. It should be stressed, therefore, that lists of references are not interchangeable and must be used only with the part to which they are appended.

New records, based on recent field observations, appear with the term 'unpublished', following them. An exception has been made in the case of reference number 49; Mr R. H. Simons kindly provided us with records from the South West Africa [Namibia] Expedition of 1957.

(iv) *Additional notes*, where needed, are inset immediately below the entry concerned. Citation of a reference in the explanatory notes depends on whether it contains records (when it consists of authors' name(s), followed by the number in the terminal reference list and where necessary, after a colon, the relevant pages) or not (when it consists of authors' name(s), date of publication and where necessary, after a colon, page numbers).

Species nomenclature has been revised as far as possible and the complete author citation is given for each accepted combination. Discarded combinations under which records for the area have previously been published are no longer (unlike the arrangement for parts I and II) included as entries in the list. They, together with all other names mentioned in the species entries, are now included as a separate terminal list of cross-references. This has been a result dictated by the present systematic arrangement. At different times in the past, generic placement within families and orders has varied, so that inclusion of required cross-references within only the currently most appropriate family and/or order would not guarantee that users would readily locate them. Repetitions of cross-references in several different families or orders would have been excessively space-consuming. The problems that will arise where it is necessary to cross-reference from one family or order of the Rhodophyta to another when these are in separate published parts do not arise in connection with the present list and will be dealt with in the introduction to the first part so affected.

As with the previous parts, this list of Bangiophyceae is still preliminary in the sense that considerable reassessments of both taxonomy and nomenclature are required in this group. Within those reservations, the present list includes all traced data published up to the end of September 1978, together with additional herbarium and MSS information. Further additions from users who detect omissions or errors in the list will be welcome.

We are grateful to Mr J. F. M. Cannon, Keeper of Botany, British Museum (Natural History), for the provision of research facilities.

Species list

PORPHYRIDIALES

Porphyridiaceae

Rhodosorus marinus Geitler
Canaries (21; 27; 36).

Note. Originally described by Geitler (21) from a seawater culture from Las Palmas. Heerebout (24) has pointed out the close resemblance to this plant of the kind of 'palmella' stage produced in culture by the division of monospores formed in the older parts of the disc of *Erythrocladia.*

Goniotrichaceae

Chroodactylon

Chroodactylon has usually been referred to in the past as *Asterocytis*. Drew & Ross (1952) have clearly established that the former is the antedating valid generic name. It has long been suggested that *Chroodactylon* (as *Asterocytis*) and *Chroothece* may well be congeneric (see Pujals, 1961, for literature review). More recently, Lewin & Robertson (1971) have demonstrated that the normally filamentous *Asterocytis* [*Chroodactylon*] *ornata* (Goniotrichales) sustains morphological change when cultured at reduced salinities, forming separate unicells in groups and thereby resembling *Chroothece* (Porphyridiales). Such a relationship, known in various members hitherto placed in the two orders, led Feldmann (1955, 1967) and Dixon (1973) to propose merging the Goniotrichales into the currently accepted Porphyridiales, under the latter name.

The likelihood is that the species currently known as *Asterocytis ornata* (C. Ag.) Hamel is correctly placed in the genus now referred to as *Chroodactylon*. Ardré (4) incorrectly assumed that Drew & Ross (1952) had already made the required combination, but this is not the case. Basson (1979:67) was the first to satisfy all nomenclatural requirements.

Chroodactylon ornatum (C. Ag.) Basson
[As *Asterocytis ornata* (C. Ag.) Hamel]
Canaries (6; 7; 8; 10; 19; 40).
[As *Asterocytis ramosa* (Thwaites) Gobi]
Sierra Leone (3).

Note. Many (see Waern, 1952, for analysis of earlier opinions) have retained the name *Asterocytis* [*Chroodactylon*] *ornata* for freshwater plants and *A. ramosa* for plants from marine conditions. Presumably this is the basis for retention of *A. ramosa* in Parke & Dixon's (1976) recent version of the check-list of British marine algae, since the first diagnosis of *Asterocytis* (as *Conferva*) *ornata* by C. Agardh (1824 : 104), although brief, is not so inadequate as to be rejected particularly when clearly associated with authentic material, this having been found on examination by Hamel (1924 : 451, 452) to be the same as *A. ramosa*. Hamel (1924), Børgesen (6) and Waern (1952), despite the latter's retention of several species names for entries, inclined to the view that one species only is involved in the genus. Lewin & Robertson (1971) showed conclusively that material (named as *A. ornata* by them) collected from the seashore at La Jolla, California, could be persuaded to grow in media of one-quarter-strength seawater (but not in lower salinities); they postulated that the occurrence of *Asterocytis* forms in freshwater may relate to distinct physiological races, if not true species, within the genus. The further establishment of the relationship one way or the other requires material from freshwater to be grown in a range of salinities, as well as necessitating the repetition for other geographical areas of the culture experiments of Lewin & Robertson in order to establish that the failure to adapt to freshwater was not merely an aspect of a local physiological race. There seems no clear justification at the present time for the rejection of the use of the specific epithet *ornata* for marine material; this, as indicated by Basson (1979:67), is also the earliest name used in connection with the many 'species' of the genus now accepted here as forming a single taxon.

Goniotrichum alsidii (Zanard.) Howe
Ascension (unpublished).
Canaries (19; 29).
Gabon (31).
Gambia (33).
Ghana (29; 34; 41A).
Nigeria (29).
Mauritanie (38).
Sénégal (50).
Sierra Leone (32).
Togo (30).

[As *Goniotrichum elegans* Collins]
Sierra Leone (3).
[As *Goniotrichum elegans* (Chauv.) Le Jol.]
Canaries (6; 20; 48).
Nigeria (20).
Sénégal (20).
[As *Goniotrichum elegans* (Chauv.) Zanard.]
Canaries (46).
'. . .; Nordwestafrika; . . .' (46).

BANGIALES

Erythropeltidaceae

Erythrocladia irregularis Rosenv.
Cameroun (unpublished).
Côte d'Ivoire (28).
Gambia (33).
Ghana (28; 29).
Liberia (13; 28).
Nigeria (28).
Salvage Islands (41).
Sierra Leone (32).
Western Sahara (38).
[As *Erythrocladia subintegra* Rosenv.]
Ghana (29).
Nigeria (20; 29).
Salvage Islands (41).
Sénégal (12; 20; 29; 50).
Sierra Leone (3).

Note. From culture experiments, it has been concluded (Heerebout, 24) that *Erythrocladia irregularis*, *E. subintegra*, *E. ectozoica* Dawson and *E. polystromatica* P. Dang. are forms of a single species. Ardré (4) also indicated that the discoid thallus of *E. subintegra* might become distromatic ('*polystromatica*') with age in its central parts. Nichols & Lissant (1967) had previously reached similar general conclusions from culturing *E. subintegra* over a period of three years. They remained fairly cautious on the significance of this, preferring first to examine type materials and concluding that '. . . variations within the genus and species *E. subintegra* may at times encompass the precise characteristics of other species. It is suggested that of the described species with apparent similarities to *E. subintegra* . . ., few distinctive characters, if any, separate them.' There are many other species currently placed in *Erythrocladia* and not examined by Nichols & Lissant, by Heerebout, or by other subsequent workers. It is thus not yet clear whether those species are more appropriately placed in *Colacodictyon*, in the *Audouinella* group, or in *Erythrocladia* itself. If they are retainable in *Erythrocladia*, that genus may well consist of merely one very variable species, the type species *E. irregularis*. Since we do not have records established for the area under names other than those already cited, further detailed consideration is not really relevant, but it is clearly appropriate for us to accept that *E. subintegra* and *E. irregularis* are conspecific, the latter epithet being retained.

Erythrotrichia

Although opinions differ on the conspecificity and form range variations of members of this genus, there is general agreement that many of the previously used names are unnecessary and relate to mere growth stages. The treatment below follows Heerebout (24) in all essentials; he showed from culture experiments and literature studies that considerable doubt exists on the

validity of many characteristics previously employed taxonomically. This results in the reduction of accepted species to three (*Erythrotrichia boryana*, *E. carnea*, *E. welwitschii*), all of which have been reported for the present area.

Erythrotrichia boryana (Mont.) Berth.
Canaries (6; 23).
Mauritanie (38).
Western Sahara (38).

Note. For detailed synonymy, see Heerebout (24). Material identifiable as *Erythrotrichia boryana* may be expected further south in the present area, since Heerebout considered Baardseth's (1941) *E. tristanensis* synonymous with *E. boryana*.

Erythrotrichia carnea (Dillw.) J. Ag.
Ascension (unpublished).
Benin (28; 30).
Canaries (6; 19; 24; 29).
Cape Verde Islands (29).
Gabon (31).
Gambia (33).
Ghana (28; 29; 41A).
Liberia (13; 28).
Mauritanie (38).
Sénégal (29).
Sierra Leone (32).
Togo (28; 30).
[As *Erythrotrichia ceramicola* Aresch.]
Cape Verde Islands (5).
[As *Erythrotrichia ceramicola* (Lyngb.) Aresch.]
Cape Verde Islands (5).
[As *Erythrotrichia investiens* (Zanard.) Bornet]
Canaries (6; 18; 19).
Sierra Leone (3).
'. . . Atlantique nord (de l'Angleterre aux Canaries.' (18).
[As *Erythrotrichia kylinii* Gardn.]
Sénégal (12).

Note. Dangeard (12) had some doubt about the identity of the Sénégal specimens. He stated that they resembled *Erythrotrichia bertholdii*, except that they possessed 2–3 basal cells forming a rudimentary disc, and were very similar to *E. californica* Kylin (=*E. tetraseriata* Gardn.). However, all three names were considered by Heerebout (24) to be synonyms of *E. carnea*.

[As *Erythrotrichia obscura* Berth.]
Canaries (6; 11; 19; 23; 41).

Note. Heerebout (24) indicated that the early stages of development of '*E. bertholdii*' were always monosiphonous, with sporulation in polysiphonous plants leading to monosiphonous growths that again afterwards became polysiphonous. Hamel (1924) had earlier stated that he thought it likely that *E. bertholdii*, possessing filaments of several rows of cells, passed through '*carnea*' and '*investiens*' stages in development. We have accepted Heerebout's contention that *Erythrotrichia bertholdii*, *E. investiens*, *E. kylinii* and *E. obscura* are all applicable to growth forms within the form range of *E. carnea*, and therefore are synonyms of the latter.

Erythrotrichia welwitschii (Rupr.) Batt.
Namibia (49).
'. . . Atlantique (de l'Angleterre a l'Afrique du sud) . . .' (4).

Note. Doubt attaches to the placement of this species in the genus *Erythrotrichia* due to the reported release of the entire contents of the cell as a spore (Dangeard, 11), and the development of new plants from small cells loosened from the penetrating basal rhizoids. Ardré (4) has pointed out the close resemblance of this species to *Bangia* whilst Heerebout (24) has preferred to retain it in *Erythrotrichia* rather 'than to erect a new monotypic, closely related genus for it'. Branching in this species may be the result of *in situ* spore germination, as has been reported in *E. carnea* (Dixon & West, 1967).

Erythrotrichia sp.
Sénégal (50).

Bangiaceae

Bangia atropurpurea (Roth) C. Ag.
Nigeria (unpublished).
[As *Bangia fuscopurpurea* (Dillw.) Lyngb.]
Benin (30).
Gabon (31).
Ghana (29).
Sénégal (12; 29; 37; 50; 51).
[As *Bangia fusco-purpurea* Lyngb.]
Canaries (9).
'. . . De la Norvège aux Canaries . . .' (9).

Note. For the conspecificity of marine and freshwater species, see Geesink (1973).

Porphyra

There is a curious absence of *Porphyra* from the Gulf of Guinea and adjacent islands. The genus is represented in Sénégal and further north, and is present from southern Angola southwards. The single exception, from Cameroun, that highlights this discontinuity is the collection described by Pilger (45); it is certainly in the genus *Porphyra*. The extent and depth of recent studies in the Gulf of Guinea indicate that *Porphyra* is probably not being overlooked.

Porphyra capensis Kütz.
South West Africa (17; 43; 44; 47; 49).
[As *Porphyra* sp.]
Angola (39).

Note. Material previously attributed by us only to genus has been kindly specifically determined by Miss J. Graves.

Overall note. Several *Porphyra* species were reported from southern Africa in the nineteenth century. J. Agardh (1883) recognized just one, retaining the name *P. capensis* for a whole plexus of forms previously named, *inter alia*, *P. umbilicalis*. See Isaac (1957) and Graves (1969) for general autecological data.

Porphyra ledermannii Pilger
Cameroun (15; 37; 45).

Note. Conway *et al.* (1976) recognize seven criteria as important to delimitation of species in *Porphyra*; these relate to the macroscopic thallus. Pilger (45) gave data for only three of these criteria (gross morphology, structure, habitat) and on present grounds *P. ledermannii* hardly warrants separate recognition since the material was also sterile. The original material of *P. ledermannii* is certainly a *Porphyra* species; it is now in such a state that specific attribution is not possible. De Toni (15), who had no authentic material from which to judge, suggested some affinity with '*Porphyra carnea* Grun.' from Madeira. *Porphyra carnea* is little known; it probably relates to *P. umbilicalis* (see Piccone, 1884 : 51).

Porphyra leucosticta Thur.
Angola (26).
Canaries (4; 6; 18; 19; 41; 52).
'. . . Atlantique (de la Suède aux Canaries . . .' (4).
'. . . Atlantique nord (de la Suède aux Canaries . . .' (18).
[As *Porphyra leucosticta* J. Ag.]
Angola (25).

Porphyra umbilicalis (L.) J. Ag.
Canaries (42).
Cape Verde Islands (19; 22).
Sénégal (12).
[As *Porphyra laciniata* J. Ag.]
Cape Verde Islands (5).
'. . . Afrique méridionale . . .' (5).
[As *Porphyra laciniata* C. Ag.]
Cape Verde Islands (16).
'Throughout the Atlantic Ocean, from the Faroe Isles to the Cape of Good Hope.' (35).

Note. The northern records implicit in this generalized statement probably do relate to *P. umbilicalis*; the southern records have been shown to relate to *P. capensis* Kütz. (*q.v.*).

[As *Porphyra laciniata* (Lightf.) C. Ag.]
'Ad litora maris Atlantici, a Scotia usque ad Caput bonae spei.' (2).

Note. See note above.

[As *Porphyra vulgaris* C. Ag.]
'Throughout the Atlantic Ocean, from the Faroe Isles to Cape Horn . . .' (35).

Note. See note above.

[As *Ulva laciniata* (Lightf.) C. Ag. β. *umbilicata* (Mohr) C. Ag.]
'In mari Atlantico, a Faeroeis usque ad caput bonae spei.' (1).

Note. See note above.

[As *Wildemannia umbilicalis* (L.) De Toni]
'ad rupes in oceano Atlantico et ejus sinubus europaeis et africanis; . . .' (14).

Note. The use of the name *Porphyra umbilicalis* by Kützing (1843 : 383) for material from 'Schottland' considerably antedates J. Agardh's (1883 : 66) placement in this genus of Linnaeus's (1753 : 1163) *Ulva umbilicalis*. In making his later combination, J. Agardh gave no indication of being aware of Kützing's earlier use of the same epithet, although this may have been a purposeful act. J. Agardh is still credited with the combination in the latest version (Parke & Dixon, 1976) of the British marine algal check-list, although the species is indicated as requiring nomenclatural reinvestigation. The purely nomenclatural process of discarding the name *P. umbilicalis* on the grounds that any combination of author attributions represents confusion (Kützing did not refer to Linnaeus, and J. Agardh ignored the Kützing statement) is highly undesirable, especially when other utilizable epithets are either undistinguished or, as for example with the *P. vulgaris* C. Ag./*P. purpurea* (Roth) C. Ag. situation, of even more doubtful nomenclatural validity.

We have therefore decided only to outline the problem and to avoid a decision that involves name changing, in that none of the courses of action open to us will clarify the position. The combination *Porphyra umbilicalis* is used and understood by all, and the biological integrity of the taxon to which the name is by long custom applied is hardly in question. We trust that good sense will prevail and that the unused Kützing name will not be allowed to disturb a relatively stable situation. Even in that situation, however, there are difficulties.

Selection of the specimen to be regarded as typotype (as defined in Stearn, 1957 : 128, 129) of *Porphyra umbilicalis* (*Ulva umbilicalis* L.) is complicated. Linnaeus (1753 : 1163) is known to have utilized mainly the description and illustration provided by Dillenius (in Ray & Dillenius, 1724 : 45, 46 and tab. VII, no. 3) as the basis for *Ulva umbilicalis* L. Whilst the illustration thus has to be selected as type for that species, the specimen (typotype) on which the illustration was based remains critically important. There are three known specimens of potential importance here; all were utilized by Dillenius at different stages. The specimen in the *Historica Muscorum* Herbarium, Oxford, is not localized and cannot be directly connected with collections from Sheerness (Kent), the only locality cited by Dillenius for the species in any text. This specimen is therefore initially set on one side for typification purposes; in any case, the specimen does not accord well with the Dillenius illustration in *Historia Muscorum*. Other specimens in the William Sherard Herbarium and in the Dillenian *Synopsis* . . . Herbarium, both University of Oxford, are localized by Dillenius to Sheerness and are of importance. Druce & Vines (1907) and Clokie (1964) have emphasized that few specimens bearing dates are extant throughout the *Synopsis* Herbarium; those that are dated were mostly collected by Dillenius and placed in that Herbarium after 1723, both as illustration of the concept in the 1724 (ed. III) *Synopsis* . . . and in preparation for a proposed fourth edition. Dillenius had only been in England from August 1721 onwards and would therefore necessarily have made use of extant herbaria, supplemented by his own restricted collections from 1721 to 1724. Most of the extant herbarium material that he employed was in the fine herbarium of his patron, William Sherard; Dillenius himself added many further specimens to that herbarium.

Specimens utilized during preparation of *Synopsis* (ed. III) were both copiously annotated in in Dillenius's hand and labelled by means of excised entries from a copy of this 1724 work; this applies both to specimens already in the collections and to those added by Dillenius. Of the three specimens of *Porphyra umbilicalis* in the William Sherard Herbarium, one is lettered 'G' on sheet and labels, and bears both MS Dillenius ('Lichen marinus Lob. Ic. II. 247. J.B. III L. 39. c. 61. p. 813 C.B. Pin: 364. 2' and 'Sherness'; later 'Tremella marina umbilicata Hist.') and an excised text of *Synopsis* . . . III: 62.2 entry. The other two are not important here. It is clear that 'G' is a major specimen in context of the Dillenian concept of *P. umbilicalis* under *Ulva marina umbilicata* (*Synopsis* III, 1724) and *Tremella marina umbilicata* (*Historia Muscorum*, 1742). Probably this specimen was one of those that Dillenius did collect himself in the 1721–24 period; all annotations of the period on the specimen are in Dillenius's hand and the entries 62.2 (*Synopsis* III) and 45–46.3 (*Historia Muscorum*) both indicate '. . . observataque mihi pone Sheerness . . .'. The later annotation on the specimen by Dillenius of the name used in *Historia Muscorum* indicates that it was also consulted for the latter work. By contrast, the specimen now in the Dillenian *Synopsis* Herbarium (62.2) is simply annotated with the *Synopsis* name and without later additions; it was probably not consulted for *Historia Muscorum*.

The pre-1724 Sherardian specimen is in rather better agreement with the 1742 illustration than is the post-1724 *Synopsis* Herbarium specimen. Original drawings made by Dillenius for the *Historia Muscorum* illustrations (in BM*) show very good agreement as to the form of lobation between the original Dillenius drawing and the Sherard Herbarium specimen, whereas that between the *Synopsis* Herbarium specimen and the original drawing is not so good. This comparison is slightly complicated by alteration in the process of drawing or engraving for publication; the image is reversed and two extra small lobes are added at upper right of the published illustration. The Sherard specimen remains much nearer in overall form. It is, of course, quite possible that the *Historia Muscorum* illustration is some sort of amalgam of impressions from more than one specimen. Even in the light of that possibility, the specimen 'G' in the William Sherard Herbarium is so much nearer in form that it should be designated typotype, and we formally so designate it. In this matter, we are unable to agree with L. M. Irvine (who has annotated the Dillenian *Synopsis* Herbarium [post-1724] specimen as typotype) and even less so with Conway (1964 : 349 and pl. I, fig. 2), who has figured as typotype the *Historia Muscorum* specimen, without stating clearly that it was from that Dillenian Herbarium.

*In this publication BM = British Museum (Natural History), London.

Porphyra sp.
Mauritanie (38).
Sénégal (37; 50; 51).
Namibia (49).

Species names mentioned within species entries

Goniotrichaceae

Asterocytis
See *Chroodactylon*.
Asterocytis ornata (C. Ag.) Hamel
See *Chroodactylon ornatum* (C. Ag.) Basson.
Asterocytis ramosa *auct.*
See *Chroodactylon ornatum* (C. Ag.) Basson.
Chroothece
See *Chroodactylon*.
Goniotrichum elegans *auct.*
See *Goniotrichum alsidii* (Zanard.) Howe.

Erythropeltidaceae

Audouinella
See *Erythrocladia irregularis* Rosenv.
Colacodictyon
See *Erythrocladia irregularis* Rosenv.
Erythrocladia ectozoica Dawson
See *Erythrocladia irregularis* Rosenv.
Erythrocladia polystromatica P. Dang.
See *Erythrocladia irregularis* Rosenv.
Erythrocladia subintegra Rosenv.
See *Erythrocladia irregularis* Rosenv.
Erythrotrichia bertholdii Batt.
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia californica Kylin
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia ceramicola *auct.*
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia investiens (Zanard.) Bornet
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia kylinii Gardn.
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia obscura Berth.
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia tetraseriata Gardn.
See *Erythrotrichia carnea* (Dillw.) J. Ag.
Erythrotrichia tristanensis Baards.
See *Erythrotrichia carnea* (Dillw.) J. Ag.

Bangiaceae

Bangia fuscopurpurea *auct.*
See *Bangia atropurpurea* (Roth) C. Ag.
Porphyra carnea Grun.
See *Porphyra ledermannii* Pilger.
Porphyra laciniata *auct.*
See *Porphyra umbilicalis* (L.) J. Ag.
Porphyra purpurea (Roth) C. Ag.
See *Porphyra umbilicalis* (L.) J. Ag.
Porphyra vulgaris C. Ag.
See *Porphyra umbilicalis* (L.) J. Ag.

Tremella marina umbilicata [Dillenius]
See *Porphyra umbilicalis* (L.) J. Ag.
Ulva laciniata (Lightf.) C. Ag. β. **umbilicata** (Mohr) C. Ag.
See *Porphyra umbilicalis* (L.) J. Ag.
Ulva marina umbilicata [Dillenius]
See *Porphyra umbilicalis* (L.) J. Ag.
Ulva umbilicalis L.
See *Porphyra umbilicalis* (L.) J. Ag.
Wildemannia umbilicalis (Lightf.) De Toni
See *Porphyra umbilicalis* (L.) J. Ag.

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All references, numbered or not, are included in the single alphabetical order of this list; works that do not contain records for the area but are relevant in some other capacity are immediately identifiable in that they are not prefixed by a number.

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Christopher John Humphries

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A revision of the genus *Anacyclus* L. (Compositae: Anthemideae)

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Synopsis

The Mediterranean genus *Anacyclus* is revised. In all, nine species and three putative hybrids, grouped into two sections, are recognized. The generic status and history of taxonomic treatments of *Anacyclus* are discussed in relation to other genera of the Anthemideae. Phylogenetic relationships and the distribution of species are analysed according to the principles of Hennigian phylogenetic systematics. A key to all species, subspecies, varieties and hybrids is given, each taxon is fully described, complete synonymies are included and the relevant taxonomic characters are discussed in detail. Distribution maps for all taxa and illustrations to the species are given, excluding only *A. latealatus*, a rare endemic from Turkey. One new species and two new subspecies combinations are made, and the existence of three, previously unrecognized, hybrids is elucidated. The account ends with a list of excluded taxa and a taxonomic index.

Introduction

The genus *Anacyclus* belongs to the family Compositae tribe Anthemideae, which is restricted to the Mediterranean region and is particularly well represented in the Maghreb countries. The circumscription of the genus has been slightly reduced from that recognized by Jahandiez & Maire (1934), to eliminate those species which belong to the *Anthemis* assemblage.

The principal taxonomic problems in the genus are due mainly to the fact that not only are several of the species extremely variable and closely related annual weeds with sympatric distributions, but the generic relationships are also not at all well known. This is one of two papers dealing with the systematics and biology of *Anacyclus* (see also Humphries, in press, *a*). The nomenclature and descriptive taxonomy are in need of critical revision, and so this has been attempted in the present paper. In addition to the formal taxonomic treatment there are discussions of morphology, phytogeography and phylogeny, and to present the right context for discussion of generic delimitation an historical account is also given.

Materials and methods

The revision is based partly on my own field studies, collections and cultivated material, which are deposited at the British Museum (Natural History) (BM), and largely on herbarium material. I was able to study five of the nine species in the field, four of which have been cultivated in the greenhouses of Chelsea Physic Garden and used in experimental crossing studies (Humphries, in press, *a*). I have studied material from the following herbaria (*Index Herbariorum* abbreviations as in Holmgren & Keuken (1974): AV, B, BM, BR, C, E, FI, G, JE, K, L, LD, LE, M, MA, MPU, P, RNG, S, W, WU, Z, ZT.

The descriptions are based on both dried and living material, where available, and the variation ranges cited attempt to cover the total variation exhibited by a particular species. Abnormal values have been placed in parentheses either before or after the main range of variation. Flowering periods, chromosome numbers, ecological data, locality lists and distribution maps have been compiled almost entirely from specimens, and data from the literature has been included only when substantiated by authentic material. One new species is recognized, two hybrids are described, and several new combinations are made.

Cross-sections of cypselas were made from my own collections, softened in water, embedded in paraffin and ceresin wax, cut by microtome and stained in safranin combined with light green or Clorazal Black E.

The material examined is not normally listed after each species examined. A complete list of all herbarium specimens seen has been placed in the library of the British Museum (Natural History). Unlocalized material of any origin is omitted, except in the case of types and authentic historical material. Formal citations are given for names and authentic records which extend knowledge of ranges or taxonomy of the taxon in question.

Descriptive terminology

The descriptions and terms used in this work follow those outlined in Featherley (1954) and Stearn (1966). The terminology for outlines and plane shapes adopted is that of the Systematics

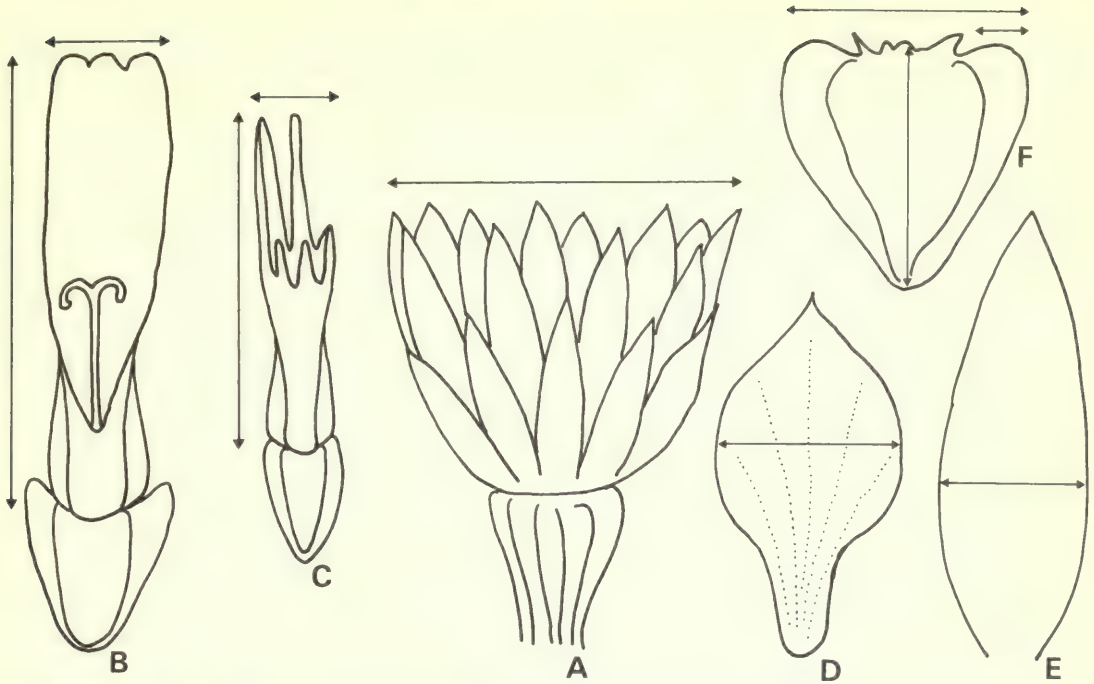


Fig. 1 Capitulum, floret & cypsela measurements: A – involucre, B – ligule, C – disc floret, D – receptacular scale, E – involucral bract, F – cypsela.

Association Committee for Descriptive Biological Terminology (1962). The capitula are usually single and terminal at the end of the peduncle. Sometimes the peduncles are structurally reduced so that the capitula are aggregated into central sessile clusters (a synflorescence) or, on rare occasions, into a single head (a syncephalum). The locations of floret and cypsela measurements are given in Fig. 1. Descriptions of variation in corolla morphology generally follow the scheme used by Jeffrey (1977).

Taxonomic concepts

The taxonomic concepts used in this revision are based on morphology, to some extent from the results of hybridization studies (Humphries, in press, *a*, *b*), distribution data and observations on ecology.

In generic revisions, as Bremer (1976) quite rightly points out, the concept of the genus, and of other categories for that matter, is seldom adequately discussed. Most flowering-plant taxonomists still follow the methods of the Aristotelian essentialist philosophical tradition as practised by Linnaeus and his generations of followers or, by contrast, by the nominalist ideals of Adanson and his contemporary protagonists, the pheneticists, as exemplified by the considerable following botanists have given to the empirical methods of Sokal & Sneath (1963) and Sneath & Sokal (1973). Consequently, in nearly all revisions, particularly in the distinctive families such as the Compositae or Umbelliferae, genera are defined on one or a few *a priori* characters (monothetic groupings) or many uncritically evaluated characters, from which totally artificial, polythetic groupings 'emerge'. This approach is of course unacceptable in phylogenetic studies, since it in no way reflects evolutionary relationships. Generic names, or those of any higher rank, can only really be applied, in phylogenetic classifications, to monophyletic groups. To produce satisfactory monophyletic groups which can be called genera (or tribes, families, etc.) the concept of 'resemblance' must be resolved, so that those features which have undergone transformation (evolution) may be recognized. Then, using only those characters which define monophyletic groups, it is possible to identify 'sister groups', i.e. those groups of species which have demonstrable shared common

ancestry (see p. 102 for discussion). In taxonomic terms, taxa of the same age, whether these be large or small groups, should have the same taxonomic rank. To complete such an ideal for the flowering plants is an awesome task, since the greatest percentage of generic names apply to either paraphyletic or polyphyletic groups (see p. 102 for discussion).

Anacyclus, in fact, was originally conceived as a paraphyletic group, but was later to contain polyphyletic elements (see p. 137 for excluded species). The circumscription of *Anacyclus* in this revision has been established according to the principles of Hennig (1965, 1966), details of which are given in the phylogenetic section (p. 102). Consequently, *Anacyclus* is defined on characters unique to those species included within the genus, as assessed by comparison with the sister group *Leucocyclus* and many other species of closely related but less easily definable genera of the northern Hemisphere Anthemideae.

It is believed that this cladistic approach to phylogenetic systematics provides the most suitable biological reference system for handling species relationships. The methods of Hennig (1965, 1966), as practised by many zoologists such as Brundin (1972) and Cracraft (1974), currently provide the most reliable cladistic techniques compatible with the concept of neo-Darwinism and with Darwin's theory of evolution by natural selection (Darwin, 1859). Consequently, it provides a natural classification in the sense that it reveals groups derived by common descent, rather than creates them artificially as is the case with essentialist or nominalist classifications based on general resemblance.

The *species* is a population concept based on a combination of marked discontinuities and, to some extent, crossing behaviour. All species of *Anacyclus* are easily defined and in several cases exhibit vicarious distribution patterns as a result of allopatric speciation. In the widespread annuals, however, vicariant patterns have been obscured as a result of migration into disturbed habitats. The *subspecies* concept has been used mainly in the sense of Du Rietz (1930) to define quantitatively distinctive populations with allopatric patterns of distribution. The term *variety* has been used to define ecological variants or locally deviating populations of a species.

Historical outline

This survey is a chronological account of contributions to the knowledge of *Anacyclus*, giving details of various changing generic and specific taxonomic concepts in the principal works from 1700 up to the present day. The taxonomic history of *Anacyclus* clearly mirrors the changing attitudes and fashions in the subject as marked by the contributions of the significant authors of the systematic tradition. To mark these changes the historical survey of *Anacyclus* is considered in four main phases: (1) from its recognizable inception as a taxonomic entity in 1700 until the publication of Linnaeus's *Species Plantarum* in 1753; (2) the contributions from the time of Linnaeus until the major contributions of perhaps the two greatest synantherologists in the post-Linnean era, Cassini and Lessing in the 1830s; (3) the expansive developments of De Candolle in the same period up to the age of the great compilations of Bentham & Hooker and Engler & Prantl in the latter half of the nineteenth century; (4) the contributions from the post-Darwinian era until the present day.

(1) The first adequate description of an *Anacyclus* species is to be found in Joseph Pitton Tournefort's *Institutiones Rei Herbariae* (1700), where 'Cotula flore luteo nudo' refers to *Chrysanthemum valentinum* in C. de L'Ecluse's *Rariorum Plantarum Historia*: 332 (1610). Tournefort did not invent the name *Anacyclus* but made the Valencian daisy the principal element of his genus *Cotula*. *Cotula* was based on a narrow, but extremely clear concept in the sense that the principal diagnostic features were well indicated. The description of the genus on page 495 in volume **1** of *Institutiones Rei Herbariae* is clearly illustrated in fig. 282 of volume **3** of the same work (Tournefort, 1700). On the evidence of this illustration and, particularly, the note on yellow ligules, the winged compressed obconical cypselas of the rays and the diminutive fruits of the central disc florets, there seems to be little doubt that the generic description and the first two phrase names of the four included species equate with the species currently called *Anacyclus radiatus* Lois. Despite such clarity, subsequent authors, as pointed out by Cassini (1825), completely ignored Tournefort's original concept of *Cotula* by not using the yellow-liguled Valencian

daisy as the principal component of the genus. Vaillant (1719), for example, changed the concept of *Cotula* entirely by applying the generic name almost exclusively to the widespread South African species, now known as *Cotula turbinata* L.: 'Cotula flore albo. Cotula africa, calyce eleganti caesio'. He included other related taxa, such as the weedy *C. coronopifolia* L., in yet another genus, *Ananthocyclus* (1719 : 289); but he correctly considered that the Valencian daisy 'Cotula flore luteo radiato' was not congeneric with *Cotula* and created a new genus *Santolinoides* to accommodate the misplaced species (1719 : 312). Like so many of the eighteenth-century genera, *Santolinoides* was an heterogeneous assemblage consisting of four distinct species, which are currently assigned to diverse genera, including *Anthemis*, *Cotula* and *Anacyclus*.

Linnaeus, in his *Hortus Cliffortianus* (1737) and *Species Plantarum* (1753), augmented Vaillant's modifications by uniting his two genera *Cotula* and *Ananthocyclus* into a wider concept of *Cotula*; in creating a new genus *Anacyclus*, he produced something akin to Vaillant's *Santolinoides* and Tournefort's original *Cotula*.

Linnaeus's definitions of *Anacyclus* were the same in both the first and fifth editions of *Genera Plantarum* (1737, 1754) and seemed to rely on Tournefort's corolla and cypsela characters as diagnostic features:

'. . . Cor. *Composita* radiata: *Corollulae Hermaphroditae* numerosae, in disco. *Femininae* quinque ad decem, in ambitu, disco vix altiores. *Propria Hermaphroditi* infundibuliformes: *limbo* quinquefido, patulo. *Feminea* ligulato: *tubo* compresso: *limbo* ovato, integro . . .Sem *Hermaphroditis* solitaria, oblonga, . . . ala latissima utrinque membranacea, apice emarginata. . . .' This description served admirably to distinguish *Anacyclus* from other members of the 'Syngenesia polygamia superflua' such as *Anthemis:* ' . . . Cor. *Composita* radiata: *corollulae Hermaphroditae* tubulosae, numerosae, in disco convexo. *Femininae* ligulatae, in radio. *Propria Hermaphroditi* infundibuliformis; *limbo* quinquedentato, erecto. *Feminae* ligulata, lanceolata, interdum tridentata . . . Sem. *Hermaphroditis* solitaria, oblonga, nuda. *Feminis* simillima hermaphroditis . . .'. Despite these precise differences Linnaeus apparently used some other character(s) in his *Species Plantarum* (1753) to diagnose the species, since a number appear to be misplaced. Thus, it is rather surprising that of the three species included in *Anacyclus*, two, *A. creticus* L. and *A. orientalis*, in fact belong to *Anthemis* on the basis of the generic descriptions given in *Genera Plantarum*; currently they are recognized as *Anthemis rigida* Sibth. & Sm. and *Anthemis orientalis* (L.) Degen respectively (Fernandes, 1976). On the same grounds two of the species placed in *Anthemis* would have been better placed in *Anacyclus*. Thus, on the basis of cypsela shape, *Anthemis pyrethrum* L. and *A. valentina* L. have a similar fruit morphology to the only other member of *Anacyclus*, *A. valentinus* L. Linnaeus understates the similarity between the two Valencian taxa when, after the description of *Anthemis valentina*, there is a note 'Affinis admodum Anacyclo valentino', the latter taxon differing only by its fewer, shorter ligules (see p. 131). Even a casual observation of the specimens available to Linnaeus shows that the only character which separated *Anacyclus* and *Anthemis* was the presence or apparent absence of ligules. This is a good example, in fact, of how the generic criteria defined in *Genera Plantarum* ed. 5 are not necessarily the same as those used in *Species Plantarum*, even though the generic epithets are the same.

(2) At the turn of the nineteenth century the major surveys of the Anthemidae which appeared in the works of Willdenow (1803) and Persoon (1807) maintained the useful generic criteria outlined by Linnaeus in his *Genera Plantarum* but still followed the designations as given in *Species Plantarum*.

Willdenow, in his *Species Plantarum* (1803 : 2171), stressed the diagnostic features at the beginning of his account: '*Recept.* paleaceum. *Pappus* emarginatus. *Sem.* lateribus membranaceus', but had devised an illogical arrangement where four species with compressed lateral winged cypselas were included in *Anthemis*. In addition to *Anthemis pyrethrum* and *A. valentina* two newly described species, *A. clavatus* and *A. tomentosa*, were included, but these are now considered to be conspecific. *Anacyclus alexandrinus* (=*Tanacetum monanthos* L.), the Egyptian and Libyan desert annual, was also described as new, and two eastern Mediterranean annuals, *A. orientalis* and *A. creticus*, were maintained in his concept of *Anacyclus*.

It was not until Brotero (*Fl. Lusit.* **1** : 239 (1804)), in a footnote to his analytical key to genera, alluded to the fact that certain taxa were artifically separated into *Anthemis* and *Anacyclus* that the

idea of re-examining the generic limits within this group emerged. He questioned the division based on the presence or absence of ray florets: 'Genus bifrons; nam accedente radio *Anthemis* est, sicut *Anthemis*, radio deficiente, *Anacyclus;* unde *Anacyclus-Valentinus*, *Anthemis-Valentina*, *Anacyclus aureus*, *Anthemis-aurea*'; but in the actual species descriptions he did a rather illogical thing: *Anacyclus* was considered to be a monotypic genus based on *A. aureus*, and the remaining taxa were placed in *Anthemis*. The use of the name *Anacyclus aureus* L. (*Mantissa* **2** : 287) appears to be based on a misidentification on Brotero's part, as De Candolle pointed out (*Flore Française* **5** : 480 (1815)), since he meant this species to be conspecific with *Anacyclus valentinus* L. Indeed, today it is known as *Chamomilla aurea* (Loefl.) Gay ex Cosson & Kralik.

Persoon (*Syn. Pl.* : 464 (1807)), adhering to the concise style typical of his diagnostic conspectus, distinguished between *Anthemis* and *Anacyclus* very precisely, in that the former genus has tetragonous or cylindrical cypselas without 'borders', whereas the fruits of the true species of *Anacyclus* are invested by a lateral membrane. This division is based on only some of the characters which define *Anacyclus* and so, although it reassociated some of the misplaced *Anacyclus* species, it had the curious effect of excluding the perennial species *Anthemis pyrethrum* and retaining the two Mediterranean species *Anacyclus creticus* and *A. orientalis*. De Candolle (1815) followed Persoon in his use of the winged fruit as the primary diagnostic feature for the genus, but is more consistent in its application. Consequently, *Anacyclus* was taken to comprise the five species *A. valentinus*, *A. radiatus*, *A. purpurascens*, *A. tomentosus* and *A. clavatus*. De Candolle remarked that 'Ces cinq plantes ne forment peut-être qu'une seule espèce. Comme je n'ose cependant l'affirmer absolument, je vaisindiquer ici un peu de mots les caractères, peut-être artificiels, par lesquels on les distingue'. He noted also that *A. purpurascens* differed from *A. radiatus* only in the red stripe of the ligule and that *A. valentinus* was a short-liguled form of the same. Indeed, *A. radiatus* and *A. purpurascens* are synonymous, as also are *A. clavatus* and *A. tomentosus*. As is demonstrated below (p. 131), European plants named *A. valentinus* L. are considered to be possible hybrids between *A. homogamos* and *A. radiatus*.

(3) The activities of the previous period and the start of the new period were punctuated by the contributions of Cassini (1825). When Cassini critically reviewed the existing literature of the Anthemideae, he offered two suggestions to improve the definition of *Anacyclus*: 'Le vrai genre *Anacyclus* tel que nous le concevons, diffère du vrai genre *Anthemis* par deux caractères principaux; 1° les ovaires obcomprimés et munis d'une large bordure sur les deux arêtes laterales; 2° les corolles du disque portant une longue corne calleuse, tres remarquable, sur leur divisions intérieures'. The main consequences when using these characters were to (i) transfer the Maghreb perennial *Anacyclus pyrethrum* from *Anthemis* (as foreshadowed by Link three years earlier (*Enum. Hort. Berol.* **2** : 344 (1822)), (ii) redescribe the genus, (iii) designate *Anthemis valentina* L. as the type of the genus, (iv) suggest a division of the genus into two sections: 'dont la première seroit caracterisée par les ovaires de la couronne aigrettes et articules avec la corolle, la seconde par les ovaires de la couronne inaigrettes et continus avec la corolle', (v) re-assign the misplaced *Anacyclus cretica* to a new genus, called *Lyonettia* Cass., as *L. pusilla* Cass. It is not clear whether Cassini considered *Anacyclus valentinus* L. and *Anthemis valentina* L. to be conspecific, but Loiseleur Deslongchamps (*Fl. Gallica* : 582 (1807)) clarified the issue when he transferred the latter species to *Anacyclus* and correctly gave it a new name, *Anacyclus radiatus* Lois.

Two major contributions providing synthetic classifications for genera of the Compositae, and the Anthemideae in particular, are found in the works of Lessing and De Candolle. This particular period was characterized by an attempt to give greater consistency to taxonomic groups and thus is marked by a wealth of new names and unusual delimitations. Lessing (1831, 1832) presented one of the more extreme views, for example, when he considered the members of the Anthemideae to belong to a much larger tribe, the Senecionideae. Species of *Anacyclus* were dispersed into two subtribes, VI Chrysanthemeae and VII Artemisieae. He divided the Chrysanthemeae still further into two groups, the Chrysanthemineae and the Anthemideae, on the basis of the absence or presence of scales (see Humphries, 1976*a*). Within group 1 Anthemideae, with receptacular scales, species of *Anacyclus* were dispersed into two genera. The perennial species, following Linnaeus' classification, was maintained as *Anthemis pyrethrum*, alongside *A. cota* L. and *A. tinctoria* L.; *Anacyclus* was taken to comprise two species only, *A. officinarum* Hayne and *A. radiatus* Lois.

The latter taxon was considered to be conspecific with *A. clavatus* Pers. Other known taxa were included in the subtribe VII Artemiseae group 1 Santolineae through the common possession of the following characters 'Capitulis multifloris; corollis staminigeris tubum plano-obcompressum et bialatum stylumque 2 – fidum gerentibus aut teretibus, si achaenium aut cor. ♀ tubulosa plano obcompressa et bialata est; rhachide bracteolata'. Necker's genus *Hiorthia* was maintained and taken to comprise *H. valentinum* (= *Anacyclus valentinus* L.), *H. aureus* (= *Anacyclus aureus* L.), *H. orientalis* (= *A. orientalis*) and *H. alexandrinus* (= *A. alexandrinus* Willd.). The most puzzling innovation was the description of a new monotypic genus *Cyrtolepis* (*Linnaea* **6** : 166 (1831); *Syn. Comp.*: 258–259 (1832)) for *C. monanthos* (L.) Less., based on *Santolina terrestris* Forsk. (= *Tanacetum monanthos* L.), a taxon clearly conspecific with *Anacyclus* (*Hiorthia*) *alexandrinus*.

De Candolle (*Prodr.* **6** : 14–18 (1838)) was considerably influenced by the work of Persoon, Cassini and Lessing when he reclassified the Anthemideae. His main contribution was to use any features which formed natural groups. The homogamous, discoid members having affinities with *Anthemis* were placed in Cassini's genus *Lyonettia* particularly to accommodate the anomalous, dwarf, eastern Mediterranean annual *Anacyclus cretica* L., then considered to be two separate species *L. pusilla* Cass. and *L. rigida* DC. Following Cassini's original suggestion, *Anacyclus* itself was divided into three sections, the first two based on the disc corolla-lobe callosities. Section 1. *Pyrethraria* DC. accommodated the perennial *Anacyclus pyrethrum* and section 2. *Diorthodon* DC. included most of the annual species: *A. pulcher* Besser ex DC. (= *A. officinarum* Hayne), *A. tomentosus* (L.) DC. and *A. clavatus* (Desf.) Pers., *A. pedunculatus* (Desf.) Pers., *A radiatus* Loisel. and *A. valentinus* L. The third section, *Hiorthia* (Necker) DC., was simply a new rank for Necker's genus to accommodate the poorly understood *A. orientalis* L. (*H. orientalis* (L.) Necker), now considered to be a discoid member of the *Anthemis montana* complex (Fernandes, 1975*a*). De Candolle removed Lessing's anomaly by uniting *Tanacetum monanthos* L. and *Anthemis alexandrina* Willd. and called it *Cyrtolepis alexandrina* (Willd.) DC.

(4) The period after De Candolle was mainly an exploration phase in which the acquisition of new material, particularly through French, English, Italian and Swedish expeditions to the Maghreb countries and the eastern Mediterranean, resulted in a wealth of notes, minor records and several descriptions of new species. At least eleven new species and many infraspecific taxa were described, particularly by Ball, Maire, Litardière, Murbeck, Boissier and Reuter, the most recent new species being *A. latealatus* Huber-Morath.

By the turn of the twentieth century *Anacyclus* had become an unnatural group, in an evolutionary sense best described as a polyphyletic genus, containing elements of the genus *Anthemis* (section *Hiorthia*, *Arthrolepis* Boiss.) and the *Achillea* assemblage (*Cyrtolepis*, *Leucocyclus* Boiss.), as in the treatment of Bentham (Bentham & Hooker, *Gen. Pl.* **2** (**1**) : 419 (1873)) and Hoffman (in Engler & Prantl, *Pflanzenfam.* (**4**) **5** : 272 (1894)). As a result of these typo-morphological classifications it has usually been reckoned that the closest affinities of *Anacyclus* are with *Anthemis*, itself a polyphyletic taxon. It is now reasonable to hypothesize that the affinities of *Anacyclus cretica* L. and *A. orientalis* L. are with *Anthemis* (Grierson & Yavin, 1975). Most people would agree that *Achillea* is a very distinct genus clearly separable from the *Anacyclus* group, but Litardière & Maire (1924) blurred the distinction when they named a new and unusual alpine species from the Atlas mountains as *Anacyclus atlanticus*. More recently, Humphries (1977) clarified the status of this species, and Grierson (1975*b*) succinctly compared and contrasted *Anacyclus* with its sister genus *Leucocyclus*. This paper now presents a complete revision of *Anacyclus* and gives an analysis of its phylogenetic relationships.

Delimitation and systematic position

The two genera *Anacyclus* and *Leucocyclus* are distinguished from related genera by their large anterior-dorsally compressed fruits with lateral wings and continuously thickened pericarp walls (Figs. 4, 5). There is little doubt that the type of fruit compression present in a number of different groups of the Compositae–Anthemideae has evolved several times (i.e. in various S. African

genera and the southern hemisphere Cotuleae), but since there is no evidence that *Anacyclus* is unnatural in its present circumscription, this observation must, for the time being, be considered a uniquely derived condition and serve to unite the two genera. The monotypic *Leucocyclus formosus* is a herbaceous endemic perennial from Turkey which resembles *Anacyclus* in most respects except that the leaves are almost vermiform, with the small segments suboppositely connected to the rhachis and divided into spinulose-dentate lobes. These genera have approximately vicarious distributions: *Anacyclus* occupies the southern, western and south-eastern Mediterranean areas, particularly in the mountains and the dry, disturbed lowlands, while *Leucocyclus* grows in the lowland montane areas in south central Turkey (Grierson, 1975*b*).

The tribe Anthemideae is usually divided into two subtribes; Anthemidinae Dumort. and Chrysantheminae Less. The Anthemidinae normally have chaff-like, scarious receptacular scales invariably subtending the ovary and, to some degree, the floret as well. The Chrysantheminae by contrast lack scales. Since this division is clearly artificial (Humphries, 1976*a*), it is inappropriate to become involved here in a detailed discussion of the subtribal classification of the Anthemideae, as all taxa allied to *Anacyclus* have receptacular scales and do not have any close allies without scales. It is therefore more appropriate to discuss the genera with which *Anacyclus* has been allied from one time to another and consider its relationships on more recent evidence.

As described in the historical section, species of *Anacyclus* have tended to be confused with taxa of the *Anthemis* assemblage rather than with any other group. Recently, Grierson (1975*a*) has suggested that *Anacyclus valentinus* L. (incl. *A. homogamos*), *A. pyrethrum* and *A. monanthos* are similar to the species of *Anthemis* section *Cota* in having a subterminal corolla. Also, the persistent tubular part of the ray floret corolla on the ripe cypselas of *Anthemis arenicola* Boiss. and *A. davisii* Yavin, a rare feature in *Anthemis*, are also found in the radiate taxa of *Anacyclus*. These trivial convergences or parallelisms are of little consequence in the formulation of phylogenetic hypotheses. Detailed studies of the fruits in genera of the Anthemideae also reveal a number of parallel morphological trends which tend to obscure the genealogical relationships in the group. As pointed out by Humphries (1977), such features include the slightly compressed cypselas of *Anthemis* section *Cota*, which differ during their development in having 7–22 ribs in the pericarp wall (Wagenitz, 1968; Kynčlova, 1970; Reitbrecht, 1974) and 5 vascular bundles (Humphries & Innes, unpublished), rather than 7–22 bundles as was wrongly assumed by the above authors.

Examination of fruit and corolla characters on a wider scale demonstrate that no case exists for making *Anthemis*, itself a polyphyletic assemblage, the sister group of *Anacyclus*. An alternative hypothesis originates from the phytochemical work of Greger (1977, 1978), where he suggests that *Anacyclus* has a cyanogenic glycoside and flavonoid phytochemical profile more closely related to *Achillea* and its allies than to species of *Anthemis*. Genera of the *Achillea* group regularly have tiny cypselas with distinct lateral ribs rather than wings, as well as unusually thin pericarp walls. It is tempting to offer a hypothesis that a group comprising *Anacyclus*, *Leucocyclus*, *Heliocauta* Humphries, *Sclerorhachis* Rech. fil. and *Achillea* L. may be recognized, as these genera all have a reduced vascular system with two lateral vascular bundles in the pericarp wall (Fig. 6), but studies on this aspect are in a preliminary state.

It is fairly clear that difficulties in forming evolutionary hypotheses of relationship at the generic level and above will persist until such a time as monophyletic groups are identified. The only recent attempts at forming natural generic groupings can be found in the work of Reitbrecht (1974; see also Heywood & Humphries, 1977), who considers that the Anthemideae consists of seven provisional groups. His 'Matricaria-gruppe' is taken to comprise *Anthemis*, *Anacyclus*, *Chamaemelum* Miller, *Cladanthus* Cass., *Matricaria* L., *Tripleurospermum* Schultz Bip., *Otospermum* Willk. and *Daveaua* Willk. ex Mariz. There seems to be no improvement in the above classification over the former groupings of Bentham (1873) and Hoffman (1894) since it is a paraphyletic assemblage without any definite character states which adequately link the genera. Such genera as *Achillea* are excluded, as they are considered to have affinities with the wind-pollinated structurally reduced members of the *Artemisia* group, as also are the southern hemisphere *Sphaeroclinium* and its allies, which Mitsuoka & Ehrendorfer (1972) have managed to hybridize with northern hemisphere members of *Matricaria*. Nevertheless, it seems probable that

once all the component members can be identified, a combination of the main elements of Reitbrecht's '*Matricaria*-gruppe' with the '*Achillea*-gruppe' will form a natural monophyletic group in the Anthemideae.

Morphology

This section provides a comparative review of the principal morphological features in *Anacyclus*, which are described formally in the taxonomic descriptions. An attempt will be made to emphasize the evolutionary trends so that an understanding of primitive and advanced character states will provide a detailed basis for the phylogenetic reconstruction (p. 105).

Habit

Most species of *Anacyclus* are annuals, a condition found in several of the north temperate genera of the Anthemideae (Heywood & Humphries, 1977). Phylogenetic analysis suggests that this is a derived condition as an adaptation for survival in dry, disturbed habitats. Several species, e.g., *A. nigellifolius*, *A. latealatus*, *A. maroccanus* and *A. linearilobus*, have restricted distributions, but the remainder have relatively wide-ranging distributions in weedy habitats. In natural sandy areas of the desert, the most extreme developments of prostrate annuals with reduced stems and leaves are seen in *A. monanthos* and to some extent in *A. homogamos*. In dry roadside or waddy habitats the vigorous, tough and leafy stems of *A. radiatus* and *A. clavatus* are among the largest growth forms to be encountered in the genus. *A. nigellifolius*, from dry rocky places in the eastern Mediterranean, represents another reduced annual habit with short erect stems (few or no branches emerging from the middle or above the centre of the main stem) and deeply dissected, small leaves.

Many species of the Anthemideae are woody or herbaceous perennials. *A. pyrethrum*, the only perennial species in *Anacyclus*, is a highly specialized montane and subalpine herbaceous perennial from open grassland and rocky places in the mountains of Morocco, Algeria and Spain. It is short-lived, with a dwarfed submerged stem fused with a long taproot to form a basal woody caudex, from which leaves and then flower-bearing peduncles emerge annually. Cross-sections of the caudex from the field suggest that most plants live for two or three or sometimes up to five years, although cultivated specimens can survive for a considerably longer period.

The leaves and peduncles emerge as a prostrate rosette from the centre of the caudex during the spring and persist until the end of the summer. The submerged caudex seems to be an adaptation to the dense snow cover and severe winters of the Atlas mountains.

Leaves

In most species the leaves are arranged alternately on the stem. However, in one or two species, e.g. *Anacyclus pyrethrum*, the leaves are so tightly whorled in a basal rosette that this arrangement is obscured (Fig. 12). Some evidence of leaf rosettes can also be seen in annuals, e.g. *A. radiatus* subsp. *radiatus* (Fig. 17) where the basal internodes are very short. *A. pyrethrum* (Figs 2 A, 12) appears to have heteromorphic leaves, because there are only massive tripinnatisect basal rosette leaves and pedunculate bracts present. A general gradation in leaf size and dissection is absent because of the reduced habit in this species.

The leaves of *Anacyclus* are invariably pinnatisect, whereby the primary divisions cut right through to the axis. The leaves range in dissection from 1- to 3-pinnatisect, depending on their position on the plant, e.g. main axis or peduncles, and, to a lesser degree, the differences between species, e.g. the small, 1- to 2-pinnatisect leaves of *A. nigellifolius* (Figs 2 J, 26). The leaves are usually differentiated into lamina and petiole, although the latter is often absent or reduced. The most distinctive petioles are the persistent cuneate types found on the rosette leaves of *A. pyrethrum* (Figs 2 A, 14) and *A. monanthos* subsp. *monanthos* (Fig. 2 B). The lamina is usually more or less flat, but is distinctly terete in the leaves of *A. pyrethrum* (Figs 2 A, 12). There is a considerable variation in leaf size, the largest leaves being found in the robust annuals *A. radiatus* subsp. *radiatus*, *A.* × *valentinus* (Fig. 2 G) and *A. linearilobus* (Fig. 2 I) and the smallest in the

Fig. 2 Leaf silhouettes: A – *A. pyrethrum*, B – *A. monanthos* subsp. *monanthos*, C – *A. maroccanus*, D – *A. radiatus* subsp. *radiatus*, E – *radiatus* subsp. *coronatus*, F – *A. clavatus*, G – *A.* × *valentinus*, H – *A. homogamos*, I – *A. linearilobus*, J – *A. nigellifolius*.

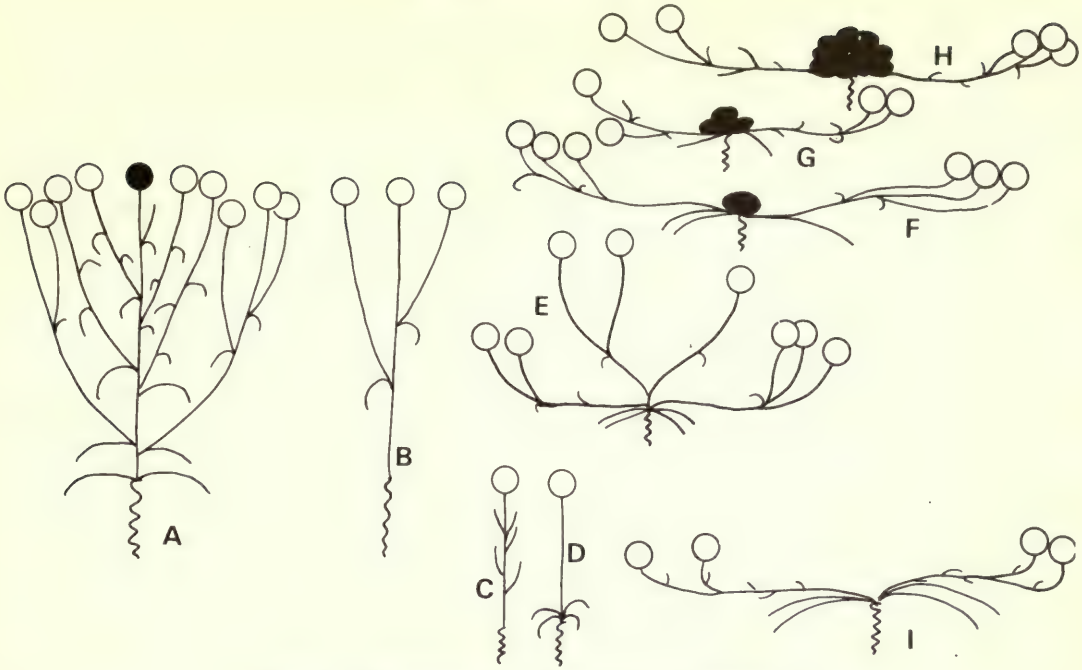


Fig. 3 Inflorescence types (see text for explanation).

eastern Mediterranean annual *A. nigellifolius* (Fig. 2 J). Measurements are given in the descriptions.

Most leaves have a distinctly herbaceous texture, but those of *A. linearilobus* are quite fleshy. *A. linearilobus* (Figs 2 J, 24) has the greatest degree of dissection in the sense that it has a small leaf area relative to the dimensions of the leaves, the wide rhachis internodes and the long, slender lobes.

Some species, e.g. *A. clavatus* (syn. *A. tomentosus*) and *A. pyrethrum* var. *depressus*, have a dense indumentum, whilst others, e.g. *A. nigellifolius* and *A. linearilobus*, are glabrous. This character is extremely variable and has little taxonomic significance. The hairs are invariably simple.

Inflorescence

A conspicuous feature in *Anacyclus* is the variation in arrangement of the capitula. These are borne singly at the end of a single peduncle (as in *A. nigellifolius*) or, more commonly, a branched peduncle (as in *A. radiatus* and *A. clavatus*), or they may be tightly grouped into a central cymose cluster with lateral peduncles emerging from the axil of the leaf or bract (as in *A. monanthos*). Examination of the different inflorescence types reveals that they represent several modifications in a distinct evolutionary trend, which is outlined in Fig. 3.

The most frequent condition is shown in Fig. 3 A; this simply consists of a fairly dense cyme with terminal capitula usually branching from the middle of a main stem. After the flowering of the first capitulum, growth is maintained by lateral alternate branches which develop beneath the capitulum and themselves eventually terminate in new capitula. The shaded capitulum in Fig. 3 A symbolizes a mature, ripe head from an early stage of the flowering period, and the unshaded heads the successive developments. This condition occurs in several species of *Anacyclus*, and it is not uncommon in some of the more robust species (e.g. *A. linearilobus*) to see a main branch lying prostrate with many successive flowering shoots emerging from its axis.

Generally, the flowering period of the most widespread weed species, *A. clavatus* and *A. radiatus*, spans several months, allowing several generations of capitula to develop on one plant. However,

by contrast, the time during which conditions are suitable for flowering may often be considerably shortened, hence curtailing the time-span for producing successive generations of capitula. In these situations there can be a considerable reduction in the number of developing branches, and the condition in Fig. 3 B is reached. In extreme situations further branch reduction and loss of leaves on the peduncles can occur to produce eventually habit types indicated in Figs 3 C, 3 D, 26. These are commonplace in the east Mediterranean endemic *A. nigellifolius* and on rare occasions in *A. clavatus* (*A. capillifolius* Maire).

A seemingly independent trend is in contraction of the stem and the peduncles. Many plants of *A. radiatus* and *A. clavatus* appear to have what looks like a protracted basal rosette, with branches of the stem and peduncles emerging nearer the base of the plant. The leaf internodes are extremely short, and the leaves emerge alternately. This condition is illustrated in Fig. 7 E. Often stem reduction is so complete that branching occurs directly from the taproot and there is an almost total loss of the larger leaves making up the rosette (e.g. in *A. monanthos* subsp. *cyrtolepidioides*). In *A. monanthos* subsp. *monanthos* stem loss is combined with peduncle reduction to produce a central acauline, sessile capitulum of the type indicated in Figs 3 F, 14. Lateral peduncles, when present, emerge from the axils of the rosette leaves or branch directly from the vestigial stem below the capitulum. A related trend is the fasciation and tumescence of peduncles as they become further reduced so that a synflorescence with 2–6 capitula is formed (Fig. 3 G). The most derived condition is produced when several or all of the capitula of the synflorescence fuse to form a syncephalum. Here, the lateral peduncles can either emerge from rosette leaf axils directly below the syncephalum or on extreme occasions even appear to emerge from the axils of involucral bracts (Fig. 3 H). In well developed specimens of *A. monanthos* subsp. *monanthos* secondary syncephala and synflorescences have been observed.

In *A. pyrethrum* (Figs 3 I, 12), the only perennial species of the genus, a rather different situation from the synflorescence and syncephalum of *A. monanthos* has developed; the stem is greatly reduced and fused directly with a long woody taproot to form a submerged basal caudex. In early spring large leaves emerge from the centre of the caudex to form a regular dense rosette. Eventually these are succeeded by a whorl of peduncles, emerging from the axils of the innermost leaves. The peduncles are commonly single-headed or only once or twice branched, providing a distinct, although somewhat contracted, flowering period. During the winter the inflorescence and leaves die right down to the ground, to be succeeded in the following season by new flowers. The development in *A. pyrethrum* differs from that in *A. monanthos* for various reasons. It shows no indication of fasciation or tumescence in the peduncles, does not have a synflorescence or syncephalum and has only one generation of flowers, never having a secondary branching point or any means of vegetative spread. The stem reduction in *A. pyrethrum* may well be an adaptation to the alpine environment in which it grows. *A. pyrethrum* is an obligate outbreeder, with a sporophytic, self-incompatible breeding system (Humphries, in press, *a*), and its flowers all exhibit the common Anthemidean, radiate gynomonoecious condition. In *A. monanthos*, stem, peduncle and capitulum modifications may be an adaptation to the hot, dry desert environment in which it is found. It is self-compatible, and its relatively inconspicuous flowers are discoid-hermaphrodite, which indicates that selfing must frequently occur. As we have seen, the evolution of the *A. pyrethrum* and *A. monanthos* inflorescences appears superficially to be very similar. However, the reduced inflorescence in each species appears to be the derivative culmination of an independent parallel trend, since they are unique conditions for the genus as a whole and indeed for the sister group of the genus. This means that the evolution of the *A. pyrethrum* rosette-type inflorescence must have passed through a number of morphological changes, if it did indeed originate from a branched cyme with long peduncles, involving the loss of a determinate capitulum, stem reduction and fusion with a woody taproot. It is interesting in this context that the extinct 'Magdeburg' officinal plant, *A. officinarum* (p. 114), which may simply be an annual derivative of *A. pyrethrum*, produced a long central stem with alternate leaves.

The prospect of secondary condensation cycles occurring in *Anacyclus*, culminating in a rosette, synflorescence or solitary capitulum, leaves the ancestral condition in some doubt, since similar morphological trends can occur in related genera. *Achillea*, for example, normally has a tight corymbose cyme but can have species with solitary capitula, as can *Leucocyclus*. More

remotely, *Anthemis* and its allies do commonly have loose cymes but exhibit a number of stem-reduction trends.

Receptacle

The receptacle is flat or very shortly conical and is, in all species, paleate, i.e. furnished with involucral bracts subtending each disc-floret. In all species these are particularly well developed, in fact perhaps the most distinctive in the Anthemideae. They show considerable variation in the genus, the toughest and most persistent being found in *Anacyclus pyrethrum* and *A. monanthos* subsp. *monanthos* (Figs 12, 14) and the most herbaceous in *A. latealatus* and *A. nigellifolius* (Fig. 26). They also show considerable variation in shape and dimensions. In *A. pyrethrum* they are distinctly obcuneate and almost as broad as wide with a tough mucronate acuminate apex, distinctly caniculate and overtopping the ripe cypsela at maturity. In *A. nigellifolius* the opposite extreme occurs, in that the receptacular scales are obovate-acuminate, somewhat flimsy and scarious and only loosely investing the cypsela at maturity.

Correlated with the variation in form is the strength of attachment to the receptacle. In all taxa the receptacular scales and cypselas are loosely attached to the receptacle. In *A. clavatus*, *A. homogamos*, and *A. radiatus* the scales are readily deciduous and will fall off the receptacle at the same time as the involucral bracts and cypselas, after the withering of the capitulum. In *A. pyrethrum* and *A. monanthos* subsp. *monanthos* they are persistent on the receptacle, and since they overtop the cypselas, the whole capitulum is dispersed as a single diaspore. Both these taxa occur in habitats with great climatic extremes, and, as a result, both have a prostrate growth habit. It seems that the mature capitula of the perennial *A. pyrethrum* are deposited a short distance away from the parental plant after it dies down for the winter, and those of the annual *A. monanthos* are left near the site of the parent plant after it disappears altogether.

Involucre

The involucre in *Anacyclus* consists of a hemispherical cup comprised of pluriseriate, brown or brownish-green bracts. Although the actual dimensions of the involucre can vary enormously, the shape can invariably be described as campanulate. The innermost bracts are usually obovate-spathulate, e.g.in *A. clavatus* (Fig.19), with a small to spreading erose apex, e.g. in *A. radiatus* (Fig. 17). Sometimes the limb is virtually absent and the innermost bracts are oblong or triangular, as in *A. pyrethrum* (Fig. 12) or *A. maroccanus* (Fig. 16). The different conditions of the involucre are fairly uniform in particular species and species groups, e.g. *A. radiatus*.

In the annuals the bracts are usually a more or less uniform light-brown colour, moderately scarious and distinctly hairy. However, the opposite extreme conditions can be seen in *A. maroccanus* and *A. pyrethrum*, which have distinctly herbaceous, green involucral bracts with narrow, dark brown margins and are usually subglabrous.

Florets

The floral characters of *Anacyclus* are particularly variable, especially in the presence and absence of ray florets, the size of ray florets, ray-floret colour, lobe size of the disc florets, the degree of compression of the corolla tube and the shape and size of corolla-tube appendages.

Most species are gynomonoecious with a single row of ligulate female florets and a central mass of perfect, hermaphrodite disc florets. *A. monanthos* and *A. homogamos*, by contrast, are monoecious with all the florets hermaphrodite. Robust, apparently discoid plants of northern Morocco and the western European Mediterranean region sometimes have a small number of extremely short female ligules, often hidden below the involucral bracts (Fig. 19). These have been considered by Maire (1932) to be a polymorphic intermediate form between the ligulate and eligulate conditions. One hypothesis to explain such variation would be that these plants represent an intermediate stage in the evolution of the monoecious discoid head. However, data from experimental, morphological and geographical studies would suggest that the heterogamous plants of *A.* × *valentinus* are more likely to be hybrids between the yellow-liguled *A. radiatus* and the discoid *A. homogamos* (see p. 128; Humphries, in press, *a*).

Within the Anthemideae the commonest ligule colour is white or creamy white. The same is true for *Anacyclus*, where white ligules are found in *A. clavatus*, *A. latealatus*, *A. linearilobus* and *A. nigellifolius*. White ligules are also found in *A. pyrethrum*, *A. radiatus* subsp. *coronatus* and *A. maroccanus*, but the lamina of the ray florets is characterized by having a deep purple stripe on the underside. This feature is always present in *A. pyrethrum* and *A. maroccanus* but is frequently absent from plants of *A. radiatus* subsp. *coronatus*. The only distinctly radiate species to have yellow ligules is *A. radiatus* subsp. *radiatus* and this, like its sister taxon, is known from several sporadic collections to have purple-striped variants frequently referred to var. *purpurascens* DC. The red-purple stripe is a feature common to a number of widely different Compositae, having been reported from *Relhania* in the Inuleae (Bremer, 1976), the Arctotideae, the Cichorioideae (e.g. *Crepis*) and the Anthemideae. There seems to be little or no information about its function; since it is only visible from above during the bud stage of flowering, Bremer (1976) has suggested that it might be a signal block for pollinators in the pre-maturation phase of anthesis.

The disc-florets are invariably yellow, infundibuliform and divided into a lower tube and an upper 5-lobed bell, which contains the anther tube. In all species, the distinction between the bell and the tube is very clear. The corolla lobes are normally regular cucullate triangular appendages, with a papillate surface on the inner face in most taxa; but in some species, e.g. the annuals *A. radiatus*, *A. clavatus*, *A. homogamos* and *A.* × *valentinus*, two of the five lobes can be distinctly longer than the other three. This feature is usually heteromorphic within a capitulum with the most zygomorphic, radiant radiate corollas towards the centre of the head and the most actinomorphic florets towards the periphery. The radiant form seems to be derived by excessive proliferation at the dorsal points of the two hooded lobes and is particularly conspicuous in *A. clavatus* (Fig. 19).

The corolla tubes of both ray and disc florets are compressed in the anterior-dorsal plane. The net result is that the centre part of the tube is somewhat oval in transverse section and is invested on either margin with a wing of varying dimensions, ranging in width from about 0·5 mm in *A. maroccanus* to 3 mm in *A. nigellifolius*. In most taxa the wings have more or less parallel sides and the base of the corolla tube articulates regularly with the ovary. In *A. linearilobus* (Fig. 24) the wings are somewhat rounded and the dorsal margin extends below the top of the ovary. This phenomenon is even more pronounced in *A. nigellifolius* (Fig. 26) and in *Leucocyclus formosus*, where the corolla tube forms an invaginated base shrouding the flattened cypsela on both the anterior and dorsal sides.

The styles and stamens of both the ray and the disc florets are monotonously constant throughout the genus. The anthers have very short tails consisting of slightly elongated, triangular cuneate apices. The style branches do vary somewhat in length but are invariably truncate-penicillate at the apex. Measurements are given with the descriptions.

Cypselas

Despite the pleas of Wagenitz (1976) and Roth (1977) to use the term achene (of Richard, 1808 and de Candolle, 1813) to describe the fruit derived from inferior ovaries, the term cypsela of Mirbel (1815) is used in preference to describe the bicarpellate coenocarpous inferior ovary of the Compositae (after Fahn, 1967), since it is clearly not homologous with other monospermous fruits to which the former term was originally applied by Necker (1790).

In *Anacyclus* the cypselas are essentially homomorphic although there is some tendency towards heteromorphy, simply because there is a gradual reduction in overall structure from the most elaborate fruits of the ray florets to the smaller cypselas of the central disc florets (Fig. 4). The cypselas in *Anacyclus*, as in so many other genera of the Anthemideae (Heywood & Humphries, 1977), provide the unambiguous diagnostic features of the genus. They are flattened in an anterior-dorsal plane with distinct lateral appendages. Anatomical features which appear to be confined to this genus and *Leucocyclus* include a pericarp consisting of a layer of sclerenchyma some 1–3 cells thick, sclerenchymatous ribs, and two laterally orientated vascular bundles (Fig. 5).

There is considerable variation in the general elaboration of wing shape and in the thickness, size and dimensions of the cypselas and, to a lesser extent, the pappus. Since it seems clear that

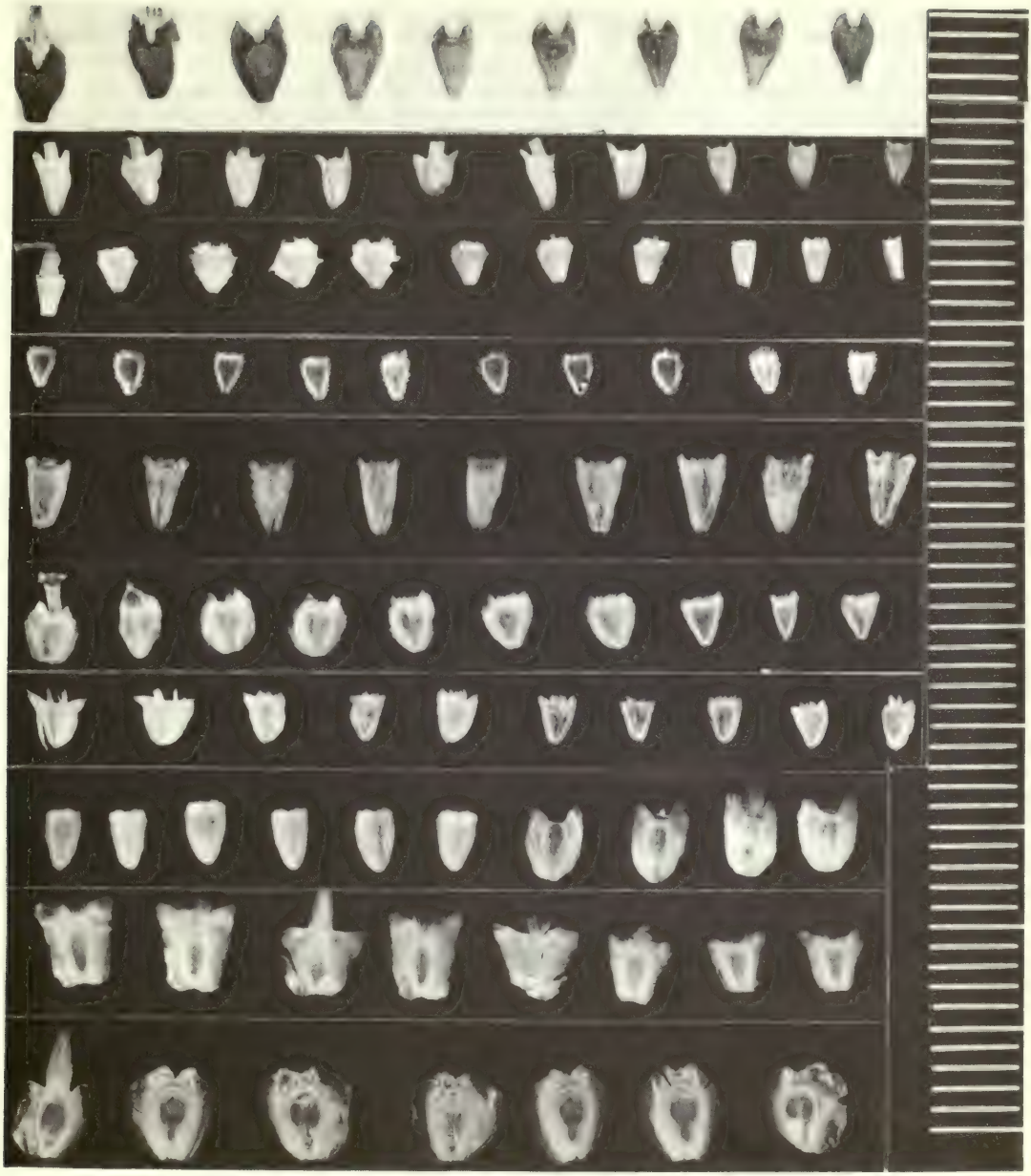


Fig. 4 Variation in cypsela morphology. An example of a transformation series where overall expansion in the wings and increase in pappus size, together with a reduction in the general form of the body, show increasing apomorphy (see Table 1). Species (from top to bottom): *A. pyrethrum* var. *pyrethrum*. *A. pyrethrum* var. *depressus*, *A. monanthos* subsp. *monanthos*, *A. maroccanus*, *A. radiatus* subsp. *radiatus*, *A. radiatus* subsp. *coronatus*, *A. clavatus*, *A. linearilobus*, *A. homogamos*, *A. nigellifolius*.

the compression of the fruit is a derived feature, then it follows that the elaboration of the wing is a consequence of the reduction of the main fruit body, since the overall dimensions of the fruit vary little within the genus. The transformation series is presented in Fig. 4, with the least elaborate fruits in *A. pyrethrum* and those with the broadest wings in *A. latealatus* and *A. nigellifolius*.

Changes accompanying the expansion of the wing include the erosion of the wing margins (as exemplified by the tough spines of *A. monanthos* and the delicate fimbriate margins of *A. maroccanus*), a general correlation between area and thickness of the wing (the broader the wings the more scarious they are), and an increase in pappus size associated again with increase in lamina area. One important species-specific characteristic is the vertically orientated auricles in *A. pyrethrum*, as distinct from the generally outwardly pointing auricles of the annual species.

A feature mentioned by Grierson (1975*a*) is the persistence of ray corolla lobes on the cypsela at maturity. Abscission of the ray corolla at the point below the ligule is frequently encountered in most of the radiate species but is particularly apparent in *A. nigellifolius*, where it appears that the corolla tube is fused with the cypsela through maturity and dispersal.

The pappus is either absent (e.g. in *A. pyrethrum*) or varies from an extremely narrow, marginal corona to a thin, lacerate scarious appendage contiguous with the wing auricles.

In transverse or longitudinal section the individual parts of the cypsela, viz. the ovary wall, the testa, the pericarp and the hypanthial tissue, are impossible to identify fully from anatomical observations. However, it is easily possible to separate the testa from the fruit wall and consider the pericarp as two layers – epicarp and mesocarp. In *Anacyclus*, most variation occurs as modifications to the mesocarp, especially in the thickness and angle of the cells in the wings and the thickness of the anterior and dorsal layers.

The pericarp and integument are often tightly attached to one another but do not coalesce. In the preparations used for Fig. 5, they are clearly seen to be separated from the fruit wall. The integument in all taxa consists of two layers, an outer epidermis with lateral or U-type thickenings and an inner layer of flattened, densely cytoplasmic cells.

The ovary is supplied with two vascular bundles lying marginally in the basal part of the rib (Fig. 6 B). They both divide at the base to provide two embryo traces and again at the apex, just below the pappus, to form two semicircular rings of corolla and stigmatic traces. The semicircular rings are asymmetrical. One of them divides three times to give one stigmatic trace and three corolla traces, whilst the other divides only twice to give two corolla traces and one stigmatic trace. Within the corolla tube the five corolla traces again divide near the base to give five outer traces.

Variation in the pericarp anatomy reflects to a great extent the differences in external morphology, the most important specific differences being the degree of sclerification of the mesocarp, the thickness of the mesocarp in the region of the anterior and dorsal faces, and the relative length of the wings and embryo. In all taxa the mesocarp parenchyma develops wall-thickening during maturation. The sclerenchyma is mostly due to scleroid development. The degree of thickening varies in different parts of the cypsela, particularly in the ribs, the faces and the apical region of the fruit wall. The most obvious and most densely thickened regions in all taxa are the basal regions of the lateral ribs in the portion surrounding or overtopping the vascular bundles. In the majority of the annual species the anterior and dorsal faces of the mesocarp are extremely thin, often only one cell thick. Nevertheless, the cells are heavily thickened to the same degree as the lateral bundles. By contrast, the cells of the pericarp in *A. pyrethrum* are only slightly thickened at maturity but are some 3–4 cells thick in the region of the faces. The epicarp epidermis is invested along the margins and at regular intervals on the surfaces with myxogenic cells (Fig. 6).

The general expansion of wing area and reduction in the main body of the fruit is associated with the development of smaller cotyledons and a thinner mesocarp.

Chromosome numbers

Somatic chromosome numbers have been investigated in five species. All of them have $2n = 18$ (see Humphries, in press, *a* and Humphries *et al.*, 1978, for review). The four annuals which have been examined, *Anacyclus radiatus* subsp. *radiatus*, *A. radiatus* subsp. *coronatus*, *A.* × *valentinus* and *A. clavatus*, all differ from the perennial *A. pyrethrum* in having three, instead of two, pairs of

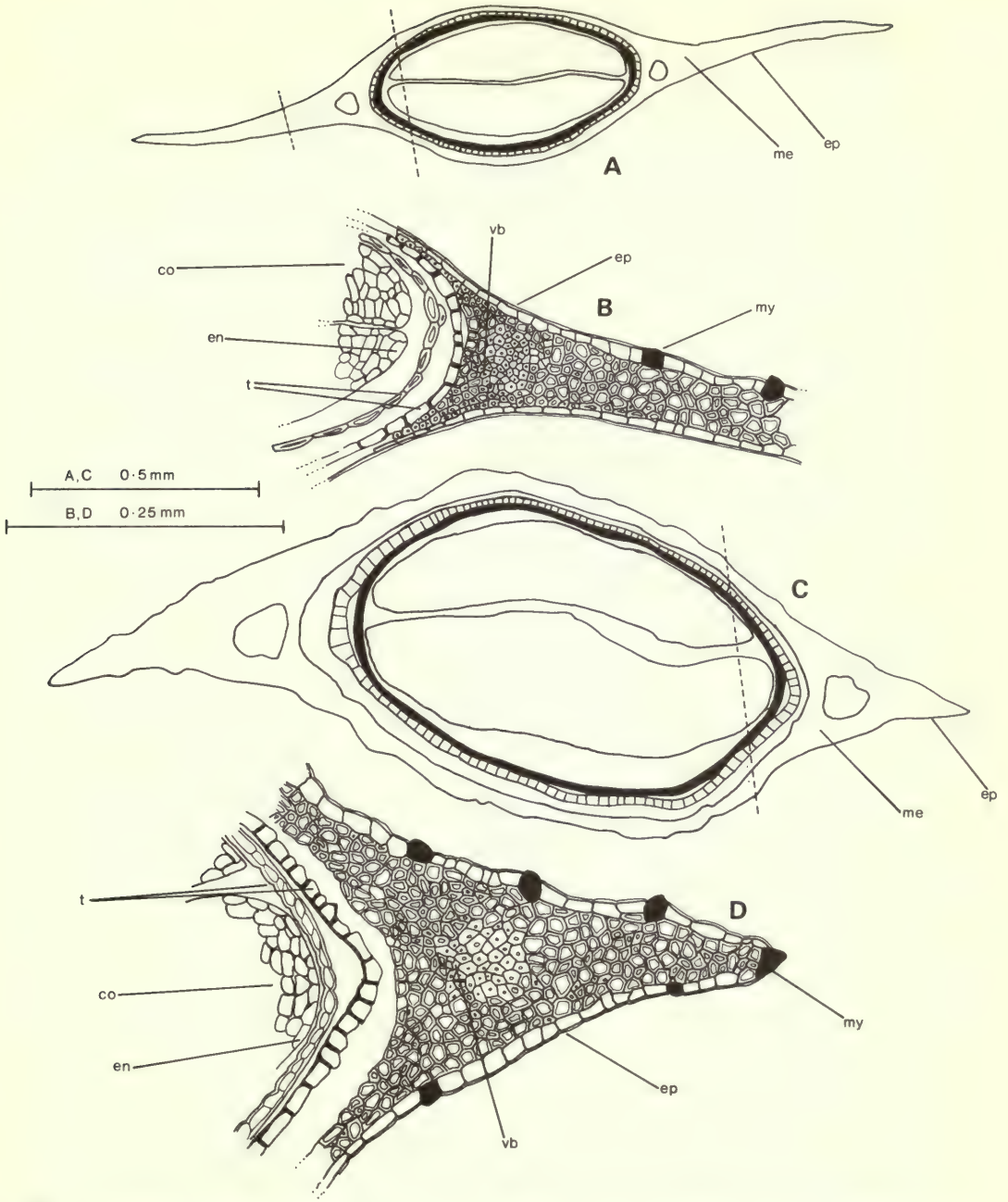
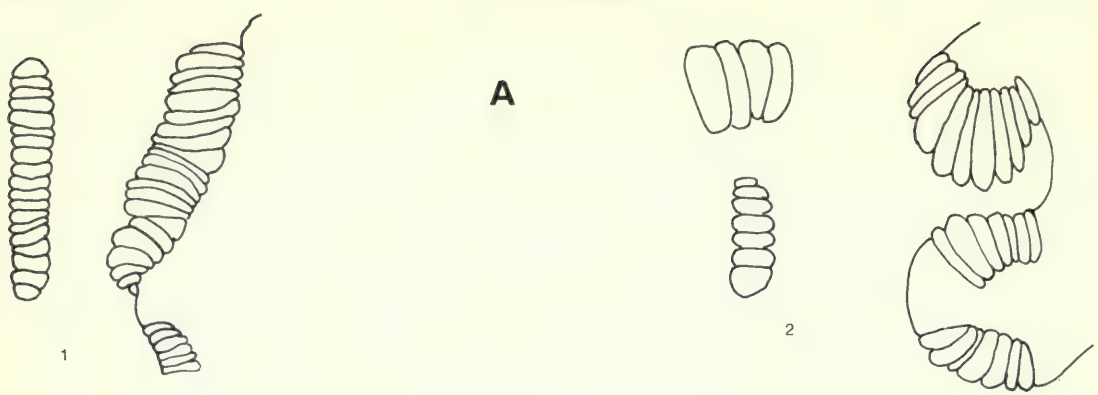


Fig. 5 Median transverse section of mature cypselas: A, B – *A. radiatus* subsp. *coronatus*; C, D – *A. pyrethrum* var. *pyrethrum*. co = cotyledons, en = endosperm, ep = epicarp, me = mesocarp, my = myxogenic cells, t = testa, vb = vascular bundles.



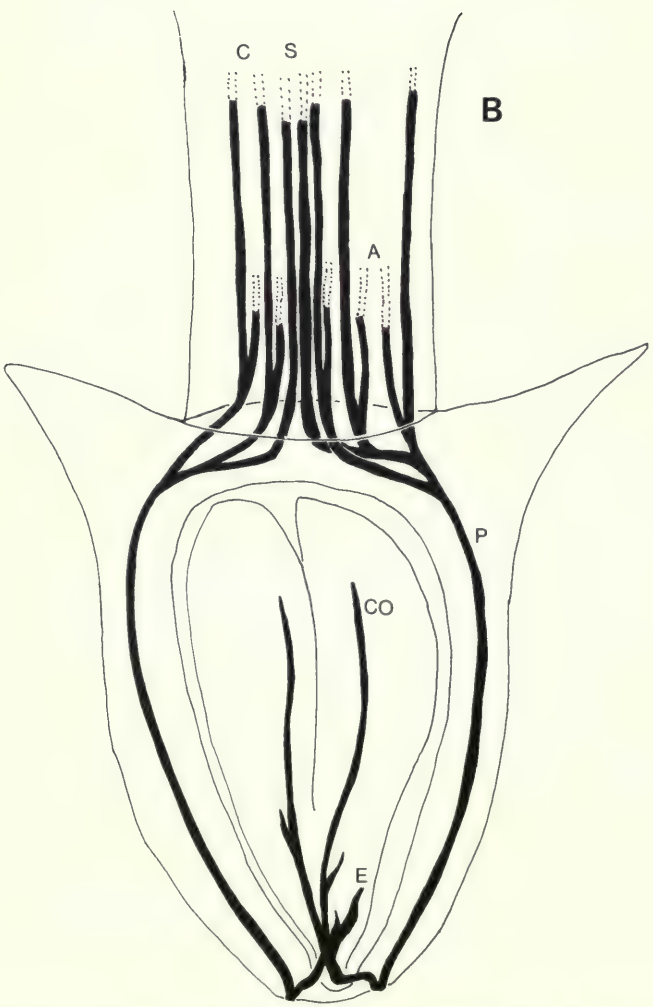


Fig. 6 A – Myxogenic cells: 1 – *A. radiatus* subsp. *radiatus*; 2 – *A. monanthos* subsp. *monanthos*. B – Vascular system in the cypsela and corolla: A – anther trace, C – corolla trace, CO – cotyledon trace, E – embryo trace, P – pericarp trace.

satellited chromosomes. This increase has been correlated with increases in the degree of chromosome banding (Schweizer & Ehrendorfer, 1977) and the self-compatible breeding system (Uitz, 1970; Humphries, in press, *a*).

Phytogeography

The approximate total range of *Anacyclus* is illustrated in Fig. 1i and the distribution of all the species on the maps in Figs 13, 15, 18, 20, 22, 23, 25 and 27 respectively. The main concentration of species is in the Maghreb region of north Africa, particularly in Morocco. It is not the concentration of species that is the main point, however, but rather how the present species relate to one another in terms of their distribution. It can be seen that several taxa, e.g. *A. radiatus* subsp. *radiatus*, *A. clavatus*, *A. homogamos* and *A.* × *valentinus*, are pernicious weeds with an apparently sympatric distribution in parts of their range, particularly in Morocco, Spain and France. However, for the most part, is it obvious that some species e.g. *A. linearilobus*, *A. latealatus* and *A. nigellifolius*, have a discrete, sometimes small vicarious pattern of distribution. It is not possible for this pattern to correspond with a general concept of a centre of origin with subsequent dispersal; but instead it indicates an allopatric process of gradual migration of *ancestors* with repeated isolation and vicariance which has eventually led to the present-day pattern of distribution. The importance of this concept, originally proposed by Croizat *et al.* (1974) and elaborated by Platnick & Nelson (1978) and Rosen (1978), has already been elegantly described by Bremer (1976, 1978) with reference to South African plant distributions; and it seems that a hypothesis that sister monophyletic groups will have vicariant distribution patterns is a general concept applicable to divergent evolutionary situations.

Some examples of vicariance are more obvious than others. *A. radiatus* subsp. *radiatus* and *A. radiatus* subsp. *coronatus* provide us with a good example of two evolving, vicarious sister taxa (Fig. 18). Their ancestor probably had a continuous distribution from north Morocco right down to the Ifni gap on the south-west Atlantic coast. Subsp. *coronatus*, the white-liguled form, has a south-west-Moroccan distribution and is particularly prominent in the Sous valley and the Atlantic seaboard from Ifni to Mogador. At the north end of its distribution there is a quite marked transition to the yellow-liguled form – the more widespread north Moroccan and western European/Mediterranean subsp. *radiatus*. It is interesting that the localized intermediates in the Mogador region have been given a range of different names reflecting their transitional nature (*A. medians* Murbeck, *A. submedians* Maire, *A. radiatus* var. *ochroleucus* Ball and *A. radiatus* var. *typicus* subvar. *concolor* Maire). Their ancestor may well have had a continuous distribution throughout their distribution range. Another example, this time of two vicarious species, is provided by *A. latealatus* and *A. nigellifolius*. They are both annuals growing on the rocky hillsides in the eastern Mediterranean (Fig. 27). *A. latealatus* is known only from the southern Turkish steppe near Tefenni, whereas *A. nigellifolius* has a more widespread distribution in southern Anatolia, Persia and the Lebanon. Such a pattern might be interpreted as quantum speciation (Grant, 1971), where a small peripheral population has budded off from the ancestral species. A similar interpretation might be applied to *A. linearilobus*, a narrow endemic from northern Algeria (Fig. 25) which is the sister species to the more widespread weeds *A. homogamos* and *A. clavatus*.

A third and distinct vicariance pattern at a higher group rank within the genus is that of the perennial varieties of *A. pyrethrum* (sect. *Pyrethraria*) and all the annuals, which together form a monophyletic group (sect. *Anacyclus*). *A. pyrethrum* is an upland species and a characteristic component of the natural treeless, subalpine meadows and rocky habitats of the Atlas mountain ranges of central and north Morocco and in Algeria (Fig. 13). By contrast, all the annuals occupy disturbed, open, lowland habitats except those few species, e.g. *A. homogamos*, which have invaded mountain habitats as roadside weeds. There is therefore a significant distribution pattern resulting from the different ecological requirements of the sister groups.

The answer to the question of the origin of the genus *Anacyclus* will not be found by a search for its centre of distribution. Instead it is much more worthwhile to ask the question: what was the

distribution of the ancestor of the present *Anacyclus* species? By way of an answer it is likely that it was a widespread species, perhaps not so widespread as to encompass the present distribution of *Anacyclus* owing to the very weedy nature of *A. radiatus* subsp. *radiatus*, *A.* × *valentinus* and *A. clavatus*, but certainly occurring in the southern Mediterranean region from southern Turkey to the Atlantic coast of Morocco.

Phylogeny

As Bremer (1976) and Bremer & Wanntorp (1978, and in press) point out, the theory of phylogenetic systematics, as described by Hennig (1965, 1966), has had virtually no effect upon the classification of plants. In fact, most publications in botany do not use any cladistics for classification (Humphries, in press, *b*) although in my opinion there is a considerable need for them rather than for the methods of the strictly phenetic and the eclectic or evolutionary biology schools.

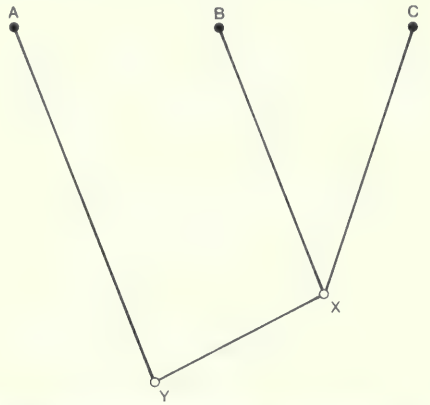


Fig. 7 The concept of phylogenetic relationship. Species B and C share a more-recent common ancestor (species X) which is not shared by species A (redrawn from Hennig, 1965).

Consequently, the construction of 'phylogenetic trees' based on ill-defined principles and the elaboration of nominalistic methods has created considerable disillusionment and disregard of sound phylogenetic discussion. This phenomenon is curious, since a glance at recent volumes of zoological, particularly entomological, literature will reveal that the principles of phylogenetic systematics are considered to be amongst the most erudite of those which advance the understanding of evolutionary relationships. I think it is necessary to re-emphasize that in the 120 years since the publication of Darwin's *Origin of Species* (1859) there has never been a serious refutation of the theory of evolution. Thus, since the advent of this theory, one of the tasks of biology has been to investigate the phylogenetic relationships between species (Hennig, 1965).

The definition of the concept 'phylogenetic relationship' is based on the fact that reproduction is sexual in most organisms, and that it usually takes place within the framework of confined reproductive communities which are isolated from one another. Speciation occurs because parts of existing reproductive communities become externally, or genetically, isolated from one another for extended periods of time. Thus, in divergent evolution, all species which exist at a given time, e.g. the present, have originated by the splitting of older reproductive communities. Thus, the concept of phylogenetic relationship can be demonstrated in a diagram, a cladogram (Fig. 7). Species B is considered to be more closely related to species C than to another species A when B has at least one ancestral species (X) in common with species C which is not ancestral to species A (see Hennig, 1965) (Fig. 7). It becomes the task of systematics, then, to determine monophyletic groups with shared common ancestry.

It is widely believed in angiosperm systematics that, since so few fossil remains are available, phylogenetic reconstruction of monophyletic groups is not reliable and possesses no method of its own. From this it follows that we can interpret the results of morphological systematics only

according to the principle that the degree of morphological relationship can be equated with the degree of phylogenetic relationship. This, of course is not so, since any concept of overall resemblance does not have the ability to distinguish between mosaic evolution, convergence and parallelism. The fundamental difference between the methods of the pheneticist and the phylogenetic systematist is that the latter breaks up the simple concept of resemblance (Hennig, 1965).

The concept of resemblance can be divided into various categories of (i) resemblance due to convergence, (ii) resemblance due to common possession of primitive (plesiomorphous) character states, and (iii) resemblance due to common possession of derived (apomorphous) character states.

Convergence occurs because similar organs have evolved adaptations to similar functions from morphological foundations in different organs, so that the character resemblances are merely analogous. Classifications based on resemblances due to convergence then produce polyphyletic rather than monophyletic groups (Fig. 8 C).

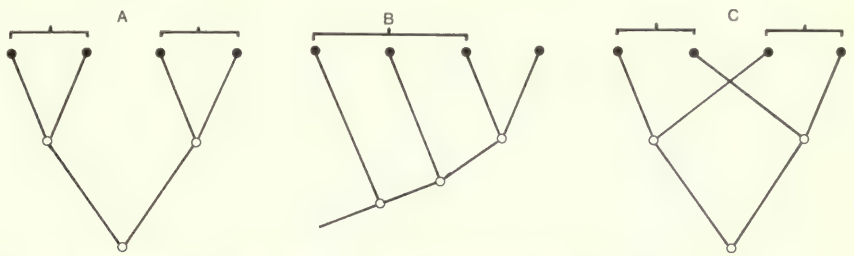


Fig. 8 Group formation and resemblance. Monophyletic groups (A) are recognized by resemblance due to synapomorphy (shared derived character states); paraphyletic groups (B) occur as a result of symplesiomorphy (shared primitive character states); and polyphyly (C) results from resemblance due to independently derived character states (redrawn from Hennig, 1965).

Even when problems of convergence can be easily removed, as of course in many cases it can, overall similarity is still not a satisfactory criterion on which to base a phylogenetic classification because it will not produce monophyletic groups. This is due to the fact that characters can remain unchanged through a number of speciation processes. Therefore the common possession of primitive (plesiomorph) characters which have remained unchanged cannot be evidence of the close relationship of their possessors. A classification based on agreement of resemblance due to shared primitive characters thus produces paraphyletic groups (Fig. 8 B). In botanical systematics there has clearly been an obsession with the possession of primitive characters in common, the obvious consequence being that a large majority of angiosperm classifications are paraphylies. It is possible to cite a whole range of examples of obvious paraphylies at various taxonomic levels, e.g. the Ranales, the Bombacaceae, the Heliantheae, *Felicia*, *Aster*, *Leucanthemum* and *Chrysanthemum* sensu lato. The supposition that two or more species are more closely related to one another, and that together they form a monophyletic group, can only be confirmed by demonstrating their common possession of derived characters (or synapomorphies). When such characters have been demonstrated, then the supposition has been confirmed that they have been inherited from an ancestral species common to only the species showing these characters.

Once this premise has been accepted, i.e. that monophyletic groups can be recognized only when morphological resemblance is due to synapomorphy, then the practical aspect can be described. Using Hennig's (1965) *Argumentation plan* (Fig. 9), every group formation of any rank must be demonstrated by synapomorphous characters. All species or groups of species have a sister group in the modern flora irrespective of divergence through time. Sister groups will then form monophyletic groups of higher rank. It follows, since evolution occurs through the change of one or more characters, that any one particular character must always occur in a more primitive (relatively plesiomorphous) condition in one group than its sister group. The same is true for the other group with regard to other characters. Therefore, it follows that there is a mosaic distribution, or heterobathmy, of character states in any group and there can be *no solely primitive or solely*

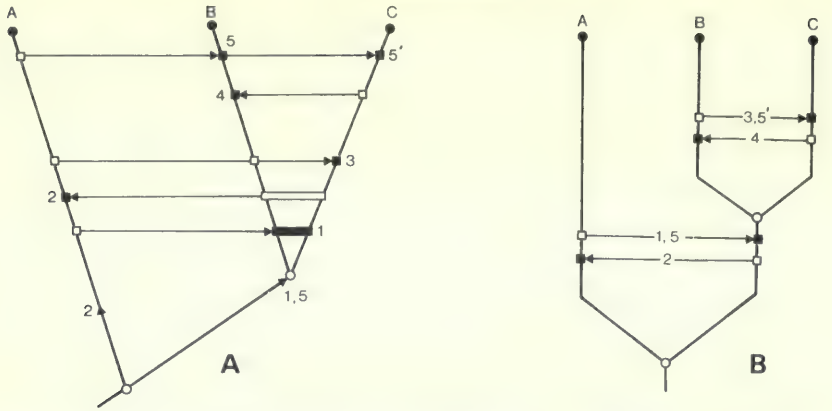


Fig. 9 Argumentation plan for phylogenetic hypotheses (□ plesiomorph, ■ apomorph) Sister-groups are established on the distribution of relatively apomorphous and relatively plesiomorphous characters. Characters 2, 3 and 4 demonstrate autapomorphous changes for the establishment of species A, B and C; character 1 demonstrates the synapomorphous feature which establishes that B and C share a more recent common ancestry than either do with A. Character 5 demonstrates a three-state transformation series of increasing apomorphy from A to C. **A** gives the traditional cladogram as used by Hennig, **B** gives a simplified 'Candelabra' version as used in this work (redrawn from Hennig, 1965).

derivative group. The aim of this method then is to produce the best, internally consistent hypothesis as to the primitive or derivative condition of each character state. The character-state conditions in *Anacyclus* are listed in Table 1, and the distribution of these characters in the species are given in the data matrix in Table 2.

Table 1 Plesiotypic and apotypic character states employed in Fig. 10

Character	Character state: Plesiotypic (—)	Apotypic (+)
Habit		
1 Duration	perennial/biennial	annual
2 Stolons	absent	present
3 Secondary thickening	present	absent
4 Main axis internodes	present	absent
Root system		
5 Basal caudex	absent	present
6 Rhizomes	present	absent
7 Fibrous roots	absent	present
Stems/inflorescence		
8 Stems	cauline	acauline or internodes ± absent
9 Inflorescence	branched	solitary
10 Syncephalous heads	absent	present
11 Central capitulum	present	absent
12 Central capitulum	aerial	basal
13 Stems	erect with solitary or corymbose inflorescences	reduced to a rosette of creeping corymbose laterals
14 Corymb laterals	from pedunculate bracts	from involucral bracts
15 Peduncles	terete	clavate
16 Peduncles	unthickened along their length	thickened along their length

Table 1 (*cont.*)

Character		Character state: Plesiotypic (−)	Apotypic (+)
Leaves			
17	Leaf rosette	absent	present
18	Leaves	homomorphic	heteromorphic
19	Leaves	herbaceous	fleshy
20	Sinus between 2nd-order lobes	narrow, less than 2 cm	wide, more than 2 cm
21	Basal leaf divisions	many	few
22	Basal leaf divisions	tripinnatisect	bipinnatisect
23	Leaves	vermiform	bi- or tripinnatisect
24	Terminal leaf-lobes	linear-lanceolate	oblanceolate
Capitulum			
25	Capitulum	radiate	discoid
26	Ligule colour	white above/red below	yellow above/red below, 'yellow, ''white
27	Ligules	exerted above involucral bracts	inserted below the involucral bracts
28	Disc corollas	actinomorphic	zygomorphic
29	Disc corollas	articulate	anteriorly vaginate
30	Disc corollas	articulate	posteriorly vaginate
31	Disc corolla articulation	terminal	anterior
32	Disc corolla wings	wingless	winged
33	Wings	narrow, usually parallel	large, oval
34	Receptacular scales	membranous	tough
35	Receptacular scales	unthickened	dorso/anteriorly thickened
36	Receptacular scales	oblanceolate	lanceolate
37	Scales	erect at apex	overlapping at apex
38	Involucral bracts	herbaceous	papery
39	Involucral bracts	obtuse	acuminate or long-pointed
40	Involucral bract margins	fuscate	light brown/hyaline, colourless
41	Inner involucral bracts	herbaceous	expanded, membranous and hyaline at the apex
42	Cypselas	terete	anterior-dorsally compressed
43	Cypsela wings	absent	narrow/thick 'narrow/thin '' broad/thinner
44	Cypsela wings	margins smooth	margin crispate
45	Cypsela wings	margins smooth	margin spiny
46	Cypsela auricles	absent	thick/pointed ' thin/pointed '' thin/rounded
47	Cypsela development	terete or rhomboid during development	flat throughout development
48	Pappus	absent	marginal, ' marginal coroniform '' coroniform

By using Hennig's (1965, 1966) methods, it has been possible to reconstruct a phylogenetic cladogram (Fig. 10) which provides the most parsimonious evolutionary model to account for morphological variation within this group and a basis for the interpretation of cytogenetic and biochemical data (Ehrendorfer *et al.*, 1977; Humphries in press *a*). The sister group of *Anacyclus* and *Leucocyclus* is indicated by inclusion in the diagram of other genera within the Anthemideae assemblage – a group taken to comprise *Achillea* and its allies.

Table 2 Data matrix employed in the phylogenetic reconstruction of Fig. 10

Taxon	Character (+ = apotypic; − = plesiotypic)																							
	45	35	16	14	12	10	44	41	25	27	24	20	19	33	29	21	30	9	39	15	38	36	22	46
Anacyclus pyrethrum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	(±)	−	−	−	−	−	−
A. monanthos	+	+	+	+	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
A. maroccanus	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
A. radiatus	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	±	−	−	−	+′
A. clavatus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+′	+	−	−	−	+″
A. homogamos	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
A. linearilobus	−	−	−	−	−	−	−	−	−	−	+	+	+	−	±	−	−	−	+″	+	−	−	−	+″
A. latealatus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+″
A. nigellifolius	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	−	+	−	−	+	+	+	+″
Leucocyclus formosus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	+	−	+	−	+	−	−
Anacyclus officinarum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+
A. × valentinus	−	−	−	−	−	−	−	−	−	(+)	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
A. × inconstans	−	−	−	−	−	−	−	−	±	(±)	−	−	−	−	−	−	−	−	+′	−	−	−	−	+″
	40	26	48	43	32	31	28	37	34	18	17	13	11	8	5	4	2	7	3	1	23	6	42	47
Anacyclus pyrethrum	−	−	−	+	−	+	−	+	+	+	+	+	+	+	+	+	(+)	−	−	−	+	+	+	+
A. monanthos	+	−	−	+	−	−	−	−	+	−	−	−	−	+	−	−	−	+	+	+	+	+	+	+
A. maroccanus	−	−	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. radiatus	+	+′,″	+″	+′	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. clavatus	±	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. homogamos	+	−	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. linearilobus	+	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. latealatus	+	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. nigellifolius	+	+″	+″	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
Leucocyclus formosus	+	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Anacyclus officinarum	−	−	−	+	−	+	−	+	+	+	+	−	−	−	−	−	−	+	+	+	+	+	+	+
A. × valentinus	+	−	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+
A. × inconstans	±	+″	+′	+″	+	+′	+	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+

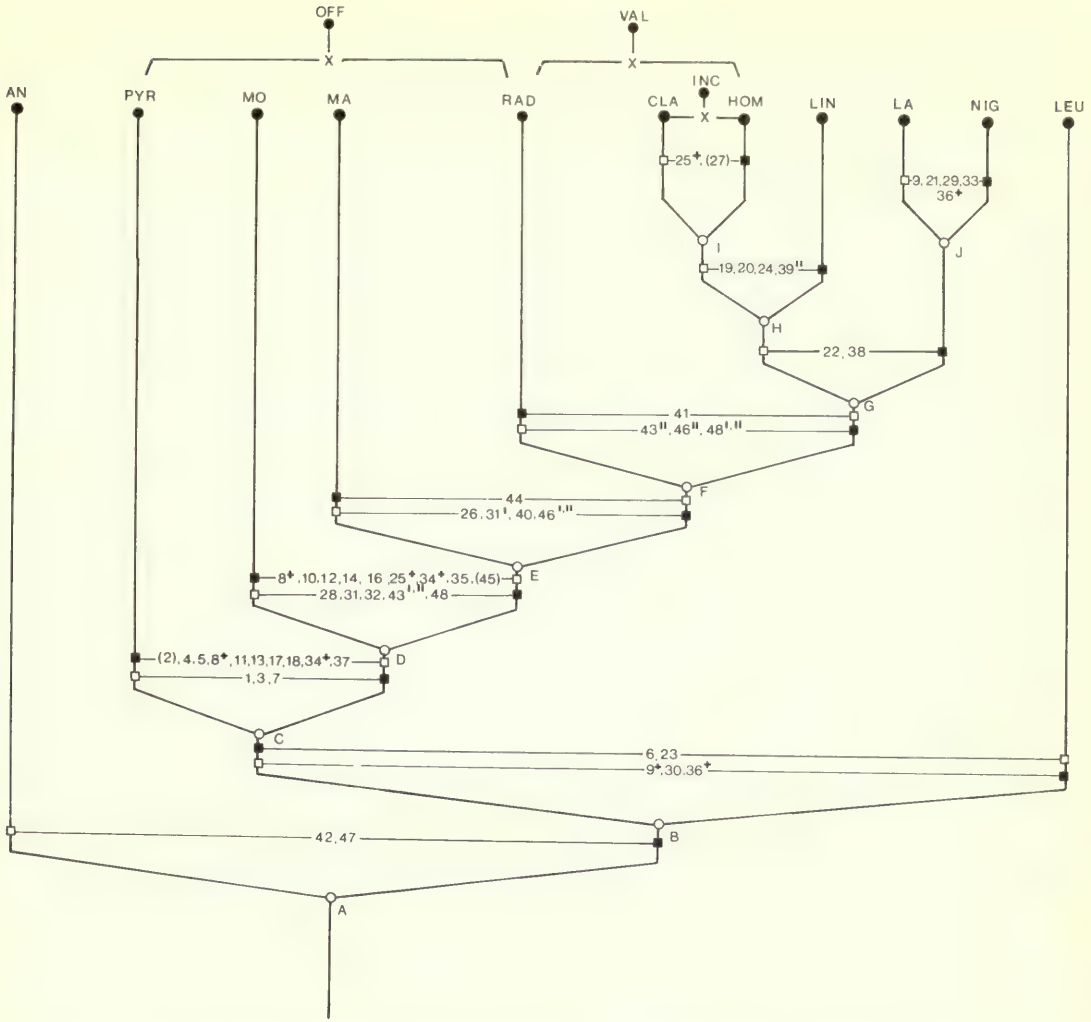


Fig. 10 Cladogram showing phylogenetic relationships in the *Anacyclus* group, based on morphological characters in Tables 1 & 2 and reconstructed according to the principles of Hennig: AN – Anthemideae (*Achillea* and its allies), PYR – *A. pyrethrum*, MO – *A. monanthos*, OFF – *A. officinarum*, MA – *A. marrocanus*, RAD – *A. radiatus*, VAL – *A.* × *valentinus*, CLA – *A. clavatus*, INC – *A.* × *inconstans*, HOM – *A. homogamos*, LIN – *A. linearilobus*, LA – *A. latealatus*, NIG – *A. nigellifolius*, LEU – *Leucocyclus formosus*.

Hennig's method makes it necessary to interpret character states either as primitive or derived conditions. This has been carried out by the principle of sister-group or related-group comparison so that commentary on some of these plesiotypic or apotypic features will help to explain the rationale behind the reconstruction of species relationships within *Anacyclus*.

In general, the systematic distribution of the majority of character states considered to be derived is consistent with the status accorded them here. Thus, for example, the apomorphic conditions found in characters 5, 10, 13, 14, 29, 30, 42, 43, 46 and 47 (Table 1) represent structural modifications which appear to be absent from all groups except those which they help to define. Therefore, *Anacyclus* and *Leucocyclus* form a monophyletic assemblage by the unique possession of the character states 42 and 47 (Tables 1 & 2).

Little more will be said about *Leucocyclus*, except to say that it is the sister-group of *Anacyclus* in the sense that it forms the second dichotomy in the cladogram (Fig. 10 B). Should this be the correct interpretation, then it follows that character states shared by *Leucocyclus* and the two Turkish *Anacyclus* species *A. nigellifolius* and *A. latealatus* (character 36) must be interpreted as independently derived to give the most parsimonious explanation of the data.

The most distinctive taxon within *Anacyclus*, and the one that is cladistically closest to the stem species C, is undoubtedly the polymorphic north African perennial *A. pyrethrum*. Nevertheless, the hypothesis that it is a very specialized derivative species within the genus, and indeed in the northern hemisphere Anthemideae as a whole, is confirmed by its possession of the autapomorphies 4, 5, 11, 13, 17, 18 and 37 (Table 2, Fig. 10 C). These include such character states as a submerged basal caudex, heteromorphic leaves, leaf rosettes and creeping inflorescences, all logically correlated adaptations to the montane habitats in which it occurs. Data on the 'Magdeburg' officinal plant *A. officinarum* are also included, since it seems to possess synapomorphies of both the perennial and annual species, superficially appearing to be an annual derivative *A. pyrethrum* but possibly being an annual hybrid between this and the commonly cultivated annual *A. radiatus* (Fig. 10).

The naturally occurring annual species clearly form a monophyletic group derived from a common ancestor with the perennials, as defined by the synapomorphies 1, 3 and 7. Within this group, *A. monanthos*, a desert plant of eastern Algeria, Tunisia, Libya and Egypt, diverges at the first dichotomy (Fig. 10 D) by possession of the autapomorphic character states 10, 12, 14 and 35. This interpretation makes it necessary to consider that the acauline habit and tough involucral scales (as in *A. pyrethrum*) and the loss of ligules (as in *A. homogamos*) are independently derived (character 25). Since *A. monanthos* seems to bear superficial resemblance to *A. homogamos* and since these species appear to show vicariant distributions (Figs 15, 23) it is tempting to consider that they share recent common ancestry. However, on the basis of such characters as its hard, obovate overtopping receptacular scales and thick, rather unspecialized cypselas which can always be readily distinguished from those of *A. homogamos*, a detailed re-interpretation of character-state trends in *A. monanthos* would have to be considered. *A. maroccanus*, the next closest annual to the stem species (Fig. 10 E), is, by comparison with the rest of the annuals, a rather unspecialized Moroccan endemic retaining a number of plesiomorphous character states, e.g. the red-pigmented undersides to the ligules and the narrow, triangular receptacular bracts of *A. pyrethrum*.

The remaining annual species form two distinct, but closely allied, groups of specialized weeds hereby designated as the '*radiatus*' and '*clavatus*' groups (Fig. 10 F, G, H). *A. radiatus* comprises two distinctive subspecies: *A. radiatus* subsp. *coronatus* has white ligules which are occasionally purple below and cypselas with an expanded lateral wing (Fig. 4); *A. radiatus* subsp. *radiatus*, by comparison, has yellow ligules which are occasionally purple below (var. *purpurascens*) but cypselas with a less widely expanded wing (Fig. 4).

A. clavatus and its allies form the most advanced group in the genus in terms of increasing apomorphy in characters 43, 46 and 48 (Tables 1, 2, Fig. 10 F). *A. clavatus* is cladistically closest to the structurally reduced weed *A. homogamos*, and examination of many different herbarium collections show that the latter species is distinguished mostly by its smaller habit, the absence of ligules, and slightly broader and more auriculate cypsela wings. It is frequently confused with *apparently* rayless forms of *A.* × *valentinus*, which are on the whole much more robust in capitulum size and general habit. Because of the short, yellow ligules in this taxon, *A.* × *valentinus* is considered to be a hybrid between *A. homogamos* and *A. radiatus* (p. 128).

A. linearilobus is a rare endemic, narrowly confined to the sand dunes of northern Algeria (Fig. 25). It can be distinguished from *A. clavatus* by the unique features of the leaf and receptacular bracts (characters 19, 20, 24 and 39).

Finally, *A. nigellifolius* and *A. latealatus*, the eastern Mediterranean vicariant species pair (Fig. 27), form the sister-group of *A. clavatus* and its immediate allies. Both species are structurally simplified annuals showing considerable decrease in leaf area and inflorescence structure, with the most apomorphous conditions apparent in the corolla and cypsela (characters 21, 22, 29, 33 and 36).

Systematic descriptions

Anacyclus L.

ANACYCLUS L., *Gen. Pl.* : 256 (1737); *Sp. Pl.* **2** : 892 (1753); *Gen. Pl.*, ed. **5** : 381 (1754). Type species: *Anacyclus valentinus* L. (= *A.* × *valentinus* L.).

Cotula Tournf., *Inst. Rei Herb.* **1** : 495 (1700), non L. Type species: *Cotula flore luteo radiato* (= *A. radiatus* Lois.).

Santolinoides Vaill., *Hist. Acad. Roy. Sci. Paris* : 312 (1719). Type species: 'Santolinoides annua, erecta, chamaemeli folio' (= *A. radiatus* Loisel.).

Cyrtolepis Less. in *Linnaea* **6** : 166 (1831): *Syn. Gen. Comp.* : 258 (1832). Type species: *Cyrtolepis monanthos* (L.) Less. (*Tanacetum monanthos* L. = *Anacyclus monanthos* (L.) Thell.).

Hiorthia Neck., *Elem.* **1** : 97 (1790); Less, *Syn. Gen. Comp.* : 258 (1832) *pro parte quoad Anacyclus valentinus* L.

Annuals and herbaceous perennials. *Stems* erect, creeping or subterranean, leafy above. *Leaves* alternate, crowded into rosettes to evenly distributed along the stem, glabrous to pubescent, bi- to tripinnatisect, flat to terete with narrow elongate segments. *Capitula* solitary, heterogamous, radiate, rarely discoid, gynomonoecious or homogamous-discoid, usually solitary at the ends of the peduncle branches or sometimes fused into a syncephalum or a syncephalous inflorescence. *Involucre* hemispherical or turbinate-hemispherical to cylindrical-campanulate; involucral bracts 3-seriate, the inner ones membranous, scarious-lacerate at the apex. Receptacle flat to shortly conical, palaeceous; the scales tough, leathery mucronate, carinate, surrounding the florets near the base, to somewhat scarious, obtuse and ± flat. *Ray florets* white, cream or yellow, sometimes with a deep red stripe below, female fertile, anterior-dorsally flattened, the tube persistent on the cypselas at maturity. *Disc florets* yellow, tubular-campanulate, 5-lobed at the apex, sometimes with 2 lobes longer and more erect than the other 3, articulating regularly with the ovary or broadened at the base and capping the ovary on the anterior side. *Cypselas* homomorphic, anterior-dorsally compressed, oblanceolate to obovate, laterally surrounded by a narrow to a very broad scarious wing. *Pappus* a unilateral corona, ± continuous with the lateral wing, otherwise absent.

Nomenclatural note: Linnaeus, in his *Species Plantarum* **2:** 892 (1753), describes three species of *Anacyclus: A. creticus*, *A. orientalis* and *A. valentinus*. The first two species now both belong to *Anthemis* L., leaving the third, *Anacyclus valentinus*, as the type of the genus. The protologue of *A. valentinus* reads as follows:

> 'ANACYCLUS foliis decompositis linearibus: laciniis divisis teretiusculis acutis, floribus flosculosis. *Hort. cliff.* 417. *Roy. lugdb.* 171. Chrysanthemum valentinum. *Clus. hist.* I. *p.* 332. Buphthalmo tenuifolio simile. *Bauh. hist.* 3. *p.* 125. *Habitat ad* Reg. Valentini *agros & vias. Confer* Anthemidem valentinam',

suggesting that the type can be based on any one of the five elements. Since the description in *Hortus Cliffortianus* : 417 (1737) is virtually unchanged from that in *Species Plantarum*:

> 'Anacyclus foliis decompositis linearibus, laciniis divisis teretiusculis acutis. Cotula flore luteo nudo. *Tournef. inst.* 495. *Boerh. lugdh.* I, p. 107. Buphthalmo tenuifolio simile, Chrysanthemum valentinum clusii. *Bauh. hist.* 3. *p.* 125. Chrysanthemum valentinum. *Clus. hist.* 1. *p.* 332. *Crescit ad margines arvorum & viarum in* Regno Valentino',

the type can be based on a specimen from this herbarium. There are three specimens in the Hortus Cliffortianus collection at the British Museum, and all of them are of the same taxon. One of them is annotated with the following note: 'Chrysanthemum valentinum clusii Hort. 332. Cotula flore luteo nudo' and agrees with both the published phrase names. The specimen is considered to be a hybrid (see p. 128) between *A. homogamos* and *A. radiatus* on account of its few depauperate female ligulate florets in the outer series of the capitulum. Nevertheless, it is a species-equivalent in nomenclatural terms and can therefore be recognized as *A.* × *valentinus* L., eliminating the need for the recognition of *A. valentinus* (L.) Cass. (based on *Anthemis valentina* L.) as the type for the genus (see p. 88).

Distribution: see Fig. 11.

Fig. 11 Approximate total range of *Anacyclus*.

Artificial key to species, subspecies, varieties and hybrids

1. Capitula homomorphic, discoid
   2. Cypselas with erose margins
      3. Central basal capitulum present; peduncles tumescent — 2a. **monanthos** subsp. **monanthos** (p. 118)
      3. Central basal capitulum absent; peduncles unthickened — 2b. **monanthos** subsp. **crytolepidioides** (p. 118)
   2. Cypselas with entire margins — 6. **homogamos** (p. 127)
1. Capitula heteromorphic, outer florets ligulate, although sometimes shortly so, so that the capitula appear discoid
   4. Ligules ± inserted and hidden in the receptacular bracts
      5. Short ligules white — ×**inconstans** (p. 130)
      5. Short ligules yellow — ×**valentinus** (p. 131)
   4. Ligules clearly visible and exerted from the receptacular bracts
      6. Ligules with a red stripe below
         7. Perennials with a distinct woody caudex
            8. Capitula 13–22 mm in diameter; old leaf-bases persistent — 1a. **pyrethrum** var. **pyrethrum** (p. 114)
            8. Capitula 7–12 mm in diameter; old leaf-bases ephemeral — 1b. **pyrethrum** var. **depressus** (p. 114)
         7. Erect or decumbent annuals with simple roots
            9. Cypsela wings distinctly crenate — 3. **maroccanus** (p. 119)
            9. Cypsela wings ± entire
               10. Ligules yellow — 4a. **radiatus** subsp. **radiatus** (p. 123)
               10. Ligules white — 4b. **radiatus** subsp. **coronatus** (p. 124)
      6. Ligules without a red stripe below
         11. Lower leaves tripinnatisect
            12. Involucral bracts broadly expanded and scarious at the apex; receptacular scales obtuse
               13. Ligules yellow — 4a. **radiatus** subsp. **radiatus** (p. 123)
               13. Ligules white — 4b. **radiatus** subsp. **coronatus** (p. 124)
            12. Involucral bracts not expanded and only narrowly scarious at the apex; receptacular scales with spines — 5. **clavatus** (p. 124)

11. Lower leaves 1–2-pinnatisect
    14. Disc corolla-tubes articulating normally with the ovary; cypselas with a lacerate corona; rhachis of upper leaves broad
        15. Cypsela wing 2·5–2·75 mm wide; Turkey — 8. **latealatus** (p. 134)
        15. Cypsela wing 0·3–0·6 mm wide; Algeria — 7. **linearilobus** (p. 131)
    14. Disc corolla-tubes expanded into an orbicular flattened disc at the base of the dorsal margin, overlapping the ovary; cypselas ecoronate; rhachis of upper leaves narrow — 9. **nigellifolius** (p. 135)

Sect. 1. **PYRETHRARIA** DC.

Anacyclus sect. *Pyrethraria* DC., *Prodr.* **6** : 15 (1838).
Anacyclus sect. *Leucocyclus* Batt. & Trabut, *Fl. Algér.* **3** : 453 (1890).

Herbaceous perennials; stem reduced to a basal, woody subterranean caudex; leaves heteromorphic, tripinnatisect to bipinnatisect; radical leaves occurring in basal rosettes. Peduncles many, prostrate, in annual rosettes. Ray florets white, with a red stripe below.

1. **Anacyclus pyrethrum** (L.) Link

Enum. Hort. Berol. Alt. **2** : 344 (1822); Cass., *Dict. Sci. Nat.* **34** : 102 (1825).
Anthemis pyrethrum L., *Sp. Pl.* : 895 (1753). Orig. coll.: Herb. Linnaeus 1016. 18. 'Pyrethrum 12' (LINN, lectotypus).
Anacyclus pseudopyrethrum Ascherson in *Bonplandia* **6:** 123 (1858) Orig. coll.: *Hohenacker*, Arznei- u. Handlespflanzen 119 (holotypus destructus).

Illustrations: Figs 2, 12. Edwards, 1799 : tab. 462; Schlectendal & Guimpal, 1833 : tab. 187; Meigen, 1842 : tab. 131e; Reichenbach, 1854 : tab. 999, fig. I, 1–3; Berg, 1861 : tab. 51, fig. 390; Artus, 1862–74 : tab. 144; Argenta, 1864 : tab. 175; Ball, 1878 : tab. 24; Bentley & Trimen, 1880 : tab. 151; Hager, 1887 : tab. 775; Pabst, 1888–90 : tab. 112; Quezel & Santa, 1963 : tab. 97, fig. 2849.

Common names: Agargarha, Agonthas, Akurkurka, Aoud el Athas, Bertram, Guenthous, Igneus, Manzanilla, Pellitory, πυρέθρυ, Piretro, Pyréthre, Pyrethri, Roman Pellitory, Spanish Chamomile, Spanish Pellitory, Tagendest, Tigenthast.

Perennial; stems fused with roots to form a submerged, woody caudex. *Leaves* heteromorphic, slightly pubescent; rosette leaves obovate in outline, petiolate, tripinnatisect, 3·0–14·0 × 0·5–3·0 cm with tiny, acute, linear ultimate segments; primary lobes in 4–9 opposite or subopposite pairs; rhachis slightly caniculate, cuneate at the base, the old veins often tough and persistent; peduncle leaves sessile, or shortly petiolate, bi- to rarely tripinnatisect, 1·0–3·0 × 0·3–1·5 cm, primary lobes in 1–6 subopposite pairs. *Inflorescence* a contracted corymbose cyme with individual creeping peduncles emerging from the centre of the caudex; each peduncle 6–30·0 cm long with 1–3 branches and terminal capitula, sparsely to densely villous, usually red, terete below the capitulum. *Involucre* 7·0–22·0 mm in diameter; involucral bracts in three rows, narrowly triangular, vivid green in the centre above, somewhat paler below with a distinct, but thin, dark-brown erose margin; receptacular scales obcuneate, carinate to canaliculate, the apices broadly obtrullate to cuspidate and overlapping the cypsela at maturity, somewhat membranous at the margin but extremely tough at the centre and above and often with a distinct central vein. *Ray florets* white, with a deep red stripe below; ligule 7·0–13·0 mm long, 3·0–4·5 mm wide, tube 3·0–5·0 mm long, 0·7–2·5 mm wide, anterior-dorsally compressed with narrow lateral wings, ♀-fertile but occasionally with vestigial anthers, articulating terminally on the ovary. *Disc florets* 3·0–5·0 mm long, anterior-dorsally compressed, lobes narrow triangular, somewhat cucullate and equal in size. *Styles c.* 3·5 mm long, the style arms 1·2–1·6 mm long. *Stamens* 3·9–4·1 mm long, anthers *c.* 2·0 mm long. *Cypselas* obcuneate to broadly ovate, 3·0–4·0 × 2·8–4·0 mm, pale grey to dark brown, sometimes purple, sphacelate; lateral wings thick, coriaceous, protruding apically with 2 ± acuminate auricles, 0·3–0·7 mm wide. *Pappus* absent.

Flowering period: Mainly May to August.

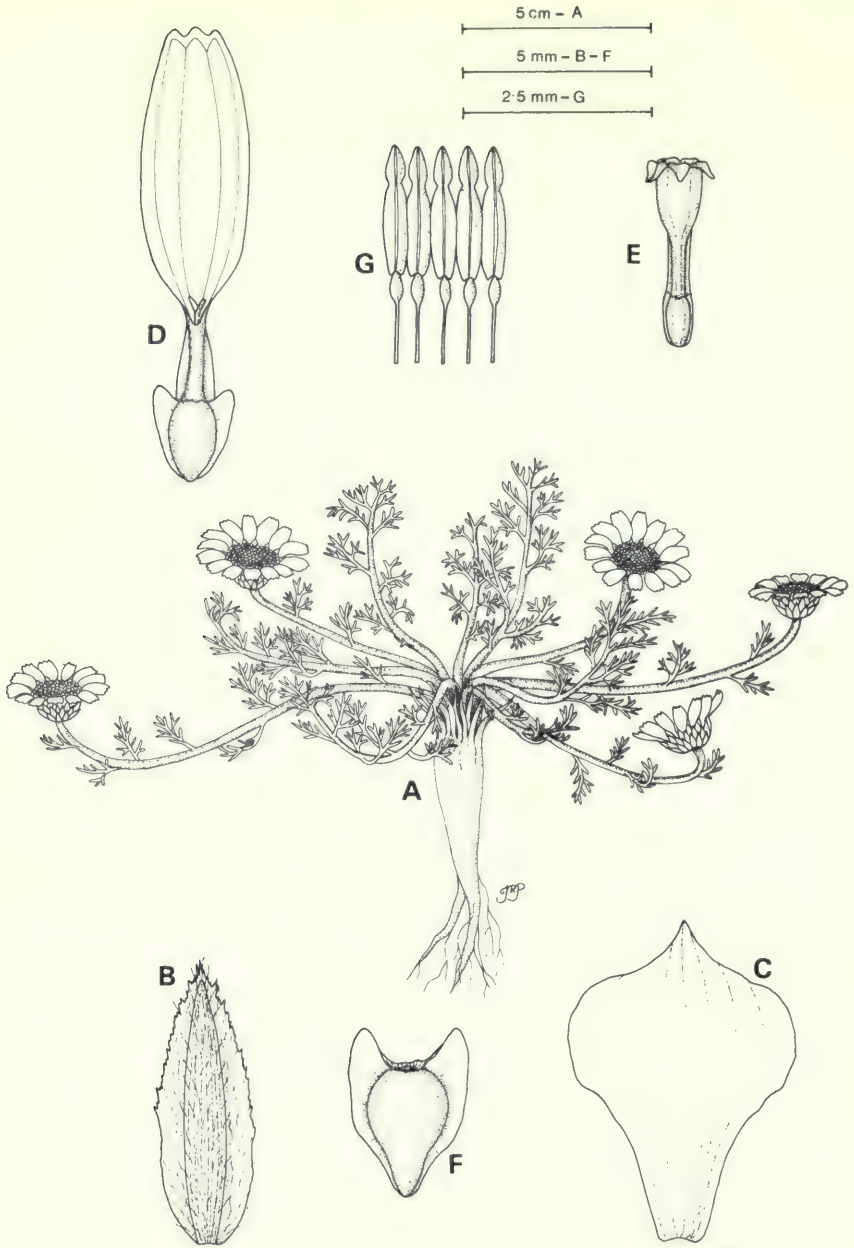


Fig. 12 *Anacyclus pyrethrum* var. *pyrethrum*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

Chromosome number: 2n = 18.

Nomenclatural note: In Linnaeus's *Species Plantarum* the description of *Anthemis pyrethrum* remains unchanged from that given in *Hortus Cliffortianus* (1737 : 414). The type specimen, which should be in Herb. Cliff. (BM) is unfortunately missing. The only other specimens corresponding with elements in the protologue are those now kept at the Linnean Society of London (LINN). There are two specimens in this collection, genus 1016 – *Anthemis*, sheets 18 and 19 (Savage, 1945), of which the first, indicated by the name '*pyrethrum*', is an inflorescence fragment

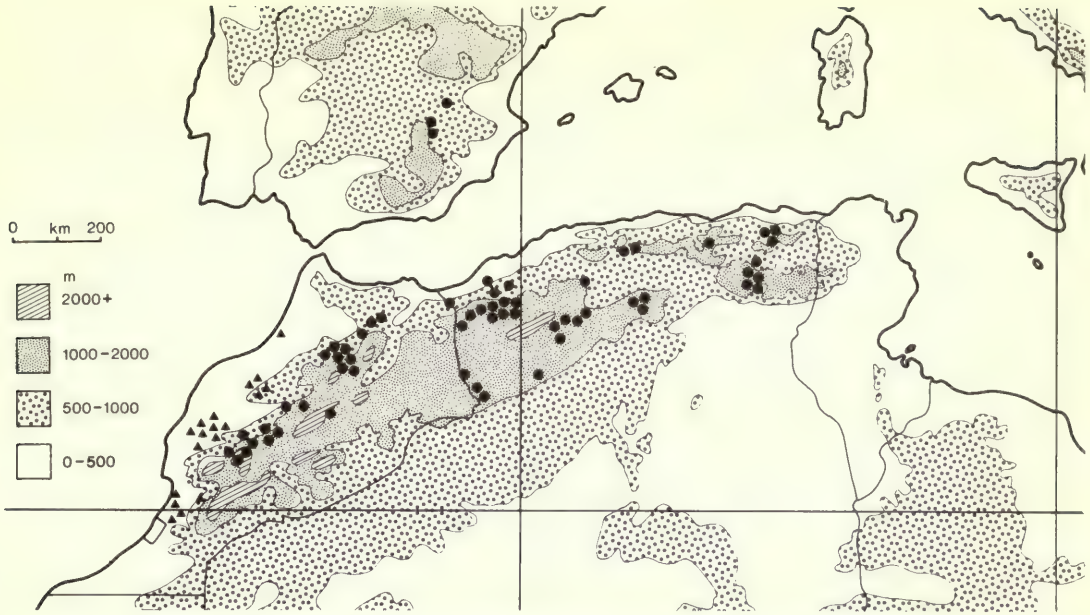


Fig. 13 Distribution of *Anacyclus pyrethrum* (●) and *A. maroccanus* (▲).

of *A. pyrethrum*. The second seems to be an aberrant cultivar. Therefore specimen 18 is chosen as the lectotype.

Variation: Anacyclus pyrethrum is perhaps the most distinctive species of the genus, since it possesses several morphological and biological features not shared by other species. Amongst the prominent morphological features are the submerged woody caudex, the heteromorphic leaves, the unusual prostrate inflorescence and the tough thickened cypselas. From a biological point of view, it appears to be the only species with a self-compatible breeding system (Uitz, 1970; Humphries, in press *a*) and occasionally has vestigial stamens in the normally female ligulate florets, suggesting its derivation from a homogamous hermaphrodite form. The cypselas are remarkably persistent at maturity and this, coupled with the fact that the receptacular scales overtop the cypselas so that they touch the next layer of bracts, makes the whole capitulum into a hard, round, almost woody head. Consequently it is often dispersed as a complete diaspore.

A. pyrethrum can be compared with the annual species *A. maroccanus*, since they share a number of plesiomorphous features, the most striking of which is the white ligules with the red stripe below. The hypothesis that they represent sister species should be tested as and when live material becomes available. The possibility that they have a recent common ancestry cannot be completely ruled out, especially in the light of their apparent vicariant distribution (Fig. 13).

A. pyrethrum is a very variable species, often occurring in small discrete montane populations. Formerly it was recognized as two species, *A. pyrethrum* and *A. depressus* Ball, the former usually being taken to comprise the more robust forms from Algeria and the eastern Moyen Atlas mountains of Morocco, which have longer stems, large capitula, longer ligules, harder fruits and generally larger vegetative parts, whereas the latter, variously called *A. feyni* Porta & Rigo, *A. pyrethrum* var. *subdepressus* Doumergue, var. *depressus* (Ball) Maire and var. *microcephalus* Maire, includes those shorter, less robust and occasionally hairier plants with small, but more numerous capitula, shorter ligules and smaller, softer cypselas, which occur in higher and drier habitats of western Algeria and the Sierra de Alcaraz, the Haut Atlas, the Anti-Atlas and the eastern Moyen Atlas. All the material of *A. pyrethrum* will fit into one of these form series; but since it is possible to find in the Moyen Atlas and parts of Algeria populations with plants which will fit into either series, to consider them as separate species or subspecies is artificial.

To emphasize the fact that there is a general reduction in various features in montane populations, two varieties are recognized.

Distribution and ecology: See Fig. 13. The distribution of *Anacyclus pyrethrum* covers a wide altitudinal range in all of the principal mountain ranges west of Guelma in Algeria in localities above 800 m. It occurs in Morocco in all exposed areas of the Moyen, Haut and Anti-Atlas and Algeria from all of the principal mountain ranges. In southern Spain all records refer to the Sierra de Alcaraz near Albacete.

The usual habitat is well drained stony ground or grassland between (800) 1100 and 3000 m, the species being particularly abundant around 1500 m.

Collections: 142 collections have been examined, mainly from the Haut and Moyen Atlas mountains and north-west Algeria.

a. Var. **pyrethrum**

Anacyclus pyrethrum var. *genuinum* Doumergue in *C.r. Ass. fr. Avanc. Sci.* **25** : 388 (1897), *nom. illeg.*
Anacyclus pyrethrum var. *typicus* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1926), *nom. illeg.*

Caudex robust. Leaf-bases persistent. Capitula 13·0–22·0 mm in diameter. Cypselas with thick wings.

Collections: Specimens mostly originate from Algeria but are common in Morocco in the more sheltered localities of the Moyen and Haut Atlas mountains.

b. Var. **depressus** (Ball) Maire

in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 768 (1934).

Anacyclus depressus Ball in *J. Bot., Lond.* : 365 (1873); *J. Linn. Soc.* (Bot.) **16** : 503–504, t. 24 (1877). Orig. coll.: *Hooker & Ball s.n.* 'In regione superiore Atlantis majoris. In convalle Aït Mesan et in jugo Tagheret a 2200 m ad 2800 m' (K, holotypus).

Anacyclus feyni Porta & Rigo in *Atti J. R. Acad. Sci. Lett. Arli Nov.* **2** : 213 (1896) Orig. coll.: *Porta & Rigo* 721, 19–27/6/1891 (FI, holotypus, B, E, G, JE, M, S, W, U, Z, isotypi) [*Anacyclus freynianus* Porta & Rigo in sched. *A. freyni*(*i*) auct.].

Anacyclus pyrethrum var. *subdepressus* Doumergue in *C.r. Ass. fr. Advanc. Sci.* **25** 2 : 388 (1897). Orig. coll.: *Doumergue s.n.*, Bedeau, El Aricha (AL, holotypus).

Anacyclus pyrethrum var. *microcephalus* Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1926). Orig. coll.: *Maire s.n.* 'Hab. in pascuis subalpinis Atlantis medii solo siliceo, ad alt. 1700–2000 m' (AL, holotypus, RAB, isotypus).

Caudex slender. Leaf bases not persistent. Capitula 7–12 mm n diameter. Cypselas with thin wings.

Collections: Specimens mostly originate from high alpine localities of the Atlas mountains, and also from exposed places in Spain and Algeria.

***Anacyclus pyrethrum* in medicine and the origin of *A. officinarum* Hayne**

Pyrethrum, commonly known as pellitory, also as Spanish or Roman pellitory, Spanish chamomile, the πυρέθρυ of Dioscorides and known in the east as Akurkurka, is the *Anacyclus pyrethrum* of modern writers. It owes its Greek and subsequent botanical names to the fiery and pungent flavour of the root (caudex) and the Latin name *Salivaria* because on chewing it causes a remarkable flow of saliva (Harley, 1876). In fact the caudex appears to be the only part which was widely used in medicine, because of its pungent efficacy in relieving toothache and promoting a free flow of saliva. Mary Grieve (1911) tells us that: 'the British Pharmacopoeia directs that it be used as a masticatory, and in the form of lozenges for its reflex action on the salivary glands in dryness of the mouth and throat. The tincture made from the dried root [caudex] may be applied to relieve the aching of a decayed tooth, applied on cotton wool, or rubbed along the gums,

and for this purpose may with advantage be mixed with camphorated chloroform. It forms an addition to many dentifrices.

'A gargle of Pellitory infusion is prescribed for relaxed uvula and for partial paralysis of the tongue and lips. To make a gargle two or three teaspoonsful of Pellitory – to be obtained from any druggist – should be mixed with a pint of cold water and sweetened with honey if desired.' Amongst its other, less important uses, it has been prescribed for relief of neuralgia, rheumatism of the head and tongue palsy. Since it is a rubefacient and a local irritant when sliced and applied to the skin, it induces heat, tingling and redness. The powered root produced a good snuff to cure chronic catarrh of the head and nostrils and to clear the brain, by exciting a free flow of nasal mucous and tears. Culpepper's herbal (see Anon, 1814) notes that *A. pyrethrum* 'is one of the best purges of the brain that grows' and is not only 'good for ague and the falling sickness [epilepsy]' but is 'an excellent approved remedy in lethargy'. After stating that 'the powder of the herb or root snuffed up the nostrils procureth sneezing and easeth the headache', it goes on to mention that 'being made into an ointment with hog's lard it taketh away black and blue spots occasioned by blows or falls, and helpeth both the gout and sciatica'. All the uses described in Culpepper were obsolete by the turn of this century. The pellitory-of-Spain was well known in the thirteenth century and was a valuable remedy for toothache with Welsh physicians (Grieve, 1911). It was familiar to Arabian writers of medicine and was still a favourite herbal remedy in the east and western Europe until the First World War, having long been an article of export from Algeria and southern Spain by way of Egypt to India.

The activity of the root appears to be due to two active crystalline resiniferous alkaloids, pellitorine and pyrethrine. *A. pyrethrum* ceased a long time ago to be used in medicine, since pellitorine, with a melting point of 22 °C, has been identified as N-isobutylamide, a reasonably powerful, poisonous insecticide. It was originally identified as N-isobutyl-cis-2-trans-6-decadieneamide but is now known to contain a mixture of at least four isomers of this product (Metcalf, 1955).

Polyacetylenes and particular amides are important taxonomically and form a distinct group of natural products characteristic of the genus. Although their biogenesis is not sufficiently clarified, it appears that most of them are derived from C_{18}-diyne-ene acid and other compounds closely related to linoleic acid and dehydromatricaria ester (Greger, 1977).

During the eighteenth and nineteenth centuries, *A. pyrethrum* was widely cultivated in European botanic gardens, particularly for its medicinal properties. In his '*Getreue Darstellung und Beschreibung der in der Arzneykunde gebräuchlichen Gewächse*, . . . part **9**', Friedrich Hayne (1825) considered that Linnaeus's concept of *Anthemis pyrethrum* (subsequently *Anacyclus pyrethrum* Link) was a 'polytypic' species containing in reality two elements, the cultivated annual 'Bertram wurzel' from Magdeburg botanic garden and the true north African perennial *A. pyrethrum*. Hayne concluded that Linnaeus's phrase name referred to the common garden form of *A. pyrethrum* (i.e. var. *depressus*), and he therefore described the annual German cultivar as a distinct species, *A. officinarum*. There are very few herbarium specimens of the latter 'species' since it appears to have been extinct since the turn of this century. The Magdeburg apothecaries cultivated the Bertram wurzel to only a limited extent (Bischoff, 1847; Harley, 1876; Hayne, 1925); and their poor knowledge of this plant, which was variously known as the Bertram root, German pellitory, African pellitory and ringblume, has led to a certain amount of misapplication of the name so that today it is incorrectly used for various species, particularly for *Anthemis altissima* Jacq. but also for *Anacyclus pyrethrum*, *A. radiatus* and *A. clavatus*. Morphological examination of *A. officinarum* (see Table 2) suggests that it is either an unusual annual derivative of *A. pyrethrum* or a hybrid between the latter species and *A. radiatus* or *A. clavatus*, since all of these are commonly cultivated together. All attempts to artificially hybridize these three species (and any other annual species) with *A. pyrethrum* have so far met with failure (Humphries, in press, *a*), so therefore the first hypothesis is currently favoured.

Illustrations of Anacyclus officinarum: Hayne, 1825 : tab. 46; Schlectendal & Guimpal, 1833 : tab. 188; Petermann, 1849 : tab. 48, fig. 374; Berg & Schmidt, 1863 : tab. 34e; Bentley & Trimen, 1880: tab. 152;

Karsten, 1880–83: 1086; Hager, 1887 : 774; Schlechtendal, Langethal & Schenk, 1887 : tab. 3039, p. 264; Karsten, 1895 : 666; Garcke, 1898 : 320; Fedtschenko & Flerov, 1910 : 969.

Sect. 2. **Anacyclus**

Anacyclus sect. *Anacyclus*, sect. typ. gen.
Anacyclus sect. *Diorthordon* DC., *Prodr.* **6** : 16 (1838).
Anacyclus sect. *Cyrtolepidia* Pomel, *Nouv. Mat. Fl. Atl.* : 53 (1874).
Anacyclus sect. *Cyrtolepis* (Less.) Batt. & Trabut, *Fl. Algér.* **3** : 452 (1890).

Annuals; stems aerial; leaves homomorphic to heteromorphic, tripinnatisect to pinnatisect; radical leaves rarely present. Peduncles one to several, erect to rarely creeping, divaricately branching. Ray florets white or yellow, with or without a red stripe below, or completely absent.

2. **Anacyclus monanthos** (L.) Thell.

in *Mém. Soc. Nat. Sci. Cherbourg*, IV, **38** : 518 (1912); C. Christensen in *Dansk Bot. Ark.* **3** : 26 (1922).
[*Tanacetum monanthemum* Vaill. in *Hist. Acad. Sci. Paris* : 282 (1719).]
Tanacetum monanthos L., *Mantissa* **1** : 111 (1767). Orig. coll.: *Forskål*, Cult. hort. Uppsala, Herb. Linnaeus 987.8 (LINN, holotypus).

Annual; stems virtually absent, reduced to a short, erect or creeping protusion on a slender taproot. *Leaves* heteromorphic; rosette leaves, when present petiolate, tripinnatisect, 3·0–10·0× 0·5–3·0 cm, with slender to sometimes broad, fleshy, acuminate ultimate segments; primary lobes in 4–7 opposite or subopposite pairs; rhachis flat, cuneate at the base, with prominent veins; pedunculate leaves sessile to petiolate, bi- or more rarely tripinnatisect, 0·5–4·2×0·2–1·2 cm, primary lobes in 2–8 subopposite pairs. *Inflorescence* a contracted cyme with radiating creeping or ascending peduncles, emerging alternately from a reduced central stem; peduncles sometimes contracted to form a central synflorescence of 2–6 capitula or a single syncephalum (1·0–) 4·0–24·0 (–35·0) cm long, with 1–9 branches and 3–6 (–12) terminal capitula, sparsely to densely villous, often inflated and sometimes fasciate and tumescent. *Involucre* 6·0–20·0 mm in diameter or up to 25·0 mm in a syncephalum; involucral bracts in 3 rows, 2·5–5·2×0·5–2·5 mm, outer series triangular, inner series broadly triangular to obcuneate, usually densely villous, usually green to brown and scarious above, somewhat fleshy and thick below, with an acuminate apex and thin laciniate margins; receptacular scales 2·8–4·5×2·2–6·0 mm, transversely broadly obovate, the apex cuspidate, caniculate, overlapping the cypsela at the apex when mature, slightly membranous at the margin but tough at the centre and above, with an obvious central vein. *Florets* discoid, hermaphrodite, homomorphic, 3·0–4·0 mm long, actinomorphic to heteromorphic radiant, where 2 corolla lobes are longer than the other 3; corolla lobes slightly cucullate, tubes anterior-dorsally compressed with lateral wings slightly broader at the base. *Styles* 2·9–3·1 mm, style arms *c.* 0·6 mm long. *Stamens* 2·8–3·5 mm long, anthers *c.* 0·5 mm long. *Cypselas* broadly obovate, 1·8–2·5×1·0–2·7 mm, usually light brown to yellow, lateral wings narrow, 0·1–0·5 mm wide, but thick, with a distinct toothed margin. *Pappus* a marginal corona or absent.

Flowering period: Mainly February–April.

Variation: *Anacyclus monanthos* is a variable species comprised of two subspecies, subsp. *monanthos* and subsp. *cyrtolepidioides*, which look quite different from one another, but are vicariant sister taxa occurring as a stepped cline running from Egypt to central and southern Algeria. The western taxon, subsp. *cyrtolepidioides*, is the least distinct, since many populations look superficially very similar to the Iberian–Moroccan species *A. homogamos*. It is tempting to consider that these two taxa may have shared common ancestry, although the hard, almost epappose cypselas with narrow, dentate lateral wings, together with the somewhat leathery, obcuneate receptacular scales of subsp. *cyrtolepidioides*, are easily distinguishable from the pappose cypselas with broad, thin, entire wings and the scarious receptacular scales of *A. homogamos*. Subsp.

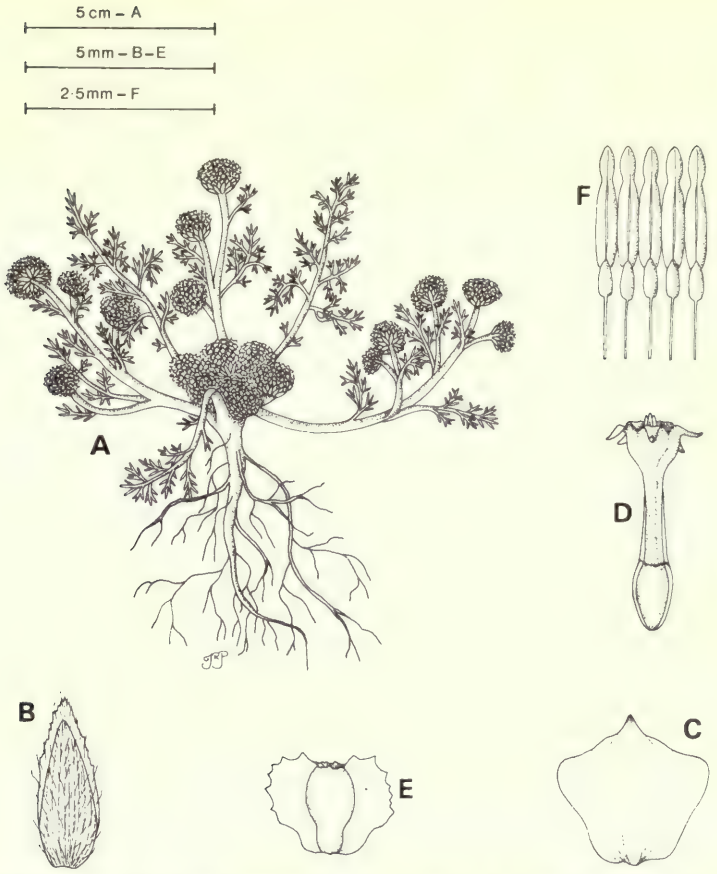


Fig. 14 *Anacyclus monanthos* subsp. *monanthos*: A – habit, B – involucral bract, C – receptacular scale, D – floret, E – cypsela, F – anthers.

monanthos, by contrast, is easily recognizable by a number of features and is usually known as *A. alexandrinus* Willd.

The habit, the type of inflorescence and the shape of the corolla lobes are the most important varying characters. Others include the hardness of the mature fruits and receptacular scales, and the size and number of capitula.

Subsp. *monanthos* is particularly well defined in both morphology and distribution. In the eastern part of its distribution it shows the most marked extremes in its acauline prostrate habit, the development of syncephalous and clustered capitula along with reduction and fasciation in the peduncles, the presence of prominent rosette leaves with very broad, cuneate rhachis bases, and the heaviest thickening in the mature fruits and receptacular scales. All these features appear to be adaptations to the extremely dry, hot conditions experienced in the desert. By contrast, subsp. *cyrtolepidioides* is less prostrate and even decumbent in Algerian and Tunisian collections, it does not have central basal clusters of capitula or syncephala, it rarely has fasciated peduncles and it sometimes has a short central stem. There is a marked absence of rosette leaves, the cypsela wings are thinner, and the cypselas are only slightly overtopped by the thickened cuspidate apices of the receptacular scales.

Both subspecies seem to occur in small discrete populations; but they come into contact in southern Tunisia and Tripolitania, where the differences between them are not quite as clear-cut as the above descriptions may suggest, several intermediate specimens having been found. Nevertheless, the vicariant, stepped-clinal variation between the extremes indicates a divergent allopatric speciation pattern.

Distribution and ecology: See Fig. 15. *Anacyclus monanthos* extends from the Nile delta in north-east Egypt to Ghardaia in the desert south of the Atlas Saharien in Algeria. Both subspecies are pioneers of sandy soils. In this context it is interesting that subsp. *cyrtolepidioides* is the dominant weed, replacing *A.* × *valentinus*, in the sandy wastelands of Biskra and Ghardaia in Algeria and around Gabes and Gafsa in Tunisia.

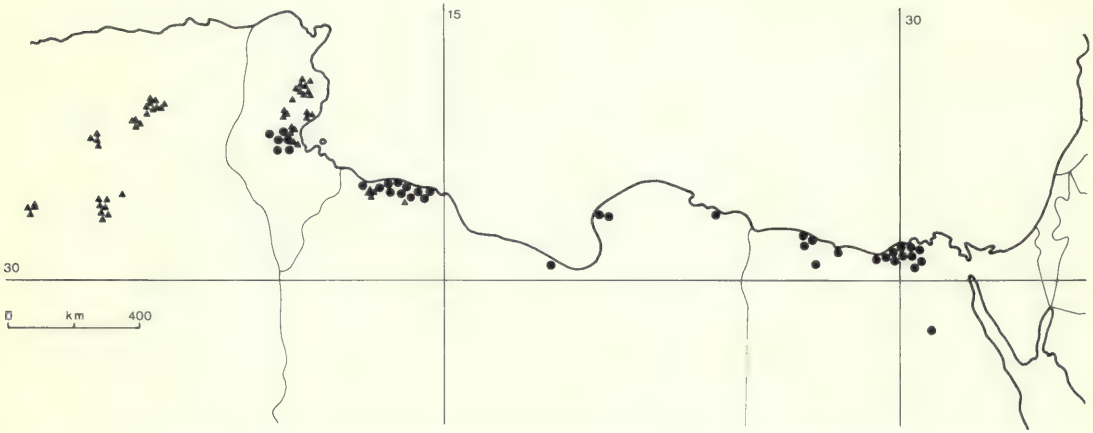


Fig. 15 Distribution of *Anacyclus monanthos* subsp. *monanthos* (●) and subsp. *cyrtolepidioides* (▲).

a. Subsp. **monanthos**

Santolina terrestris Forskål, *Fl. Aegypt.-Arab.* 147 (1775). Orig. coll.: *Forskål* (1762), Cent. 5, no. 72, Aegypto: Alexandria in vicinia columna Pompeyi (C, holotypus).
Anacyclus alexandrinus Willd., *Sp. Pl.* **3** : 2173 (1800). Orig. coll.: Herb. Willdenow 16307 (B, lectotypus).
Anthemis arabica Viv., *Fl. Lib.* : 56 (1824), non. L.
Hiorthia alexandrina (Willd.) Less., *Syn. Gen. Comp.* : 258 (1832).
Cyrtolepis alexandrina (Willd.) DC., *Prodr.* **6** : 17 (1838).
Cyrtolepis alexandrina (var.) β *glabra* DC., *Prodr.* **6** : 18 (1838).
Cyrtolepis alexandrina DC. var. nov. Coss. in *Bull. Soc. Bot. Fr.* **36** : 95 (1889).

Illustrations: Figs 2, 4, 14. Delile, 1814 : tab. 48; Gubb, 1913 : tab. 13; Quezel & Santa, 1963 : tab. 97, fig. 2850.
Common names: Sorret el Kebch.

Peduncles prostrate, emerging from the axils of the rosette leaves or from the axils of receptacular bracts of syncephalous capitula, frequently swollen and coalescing into groups of 2 or 3. Central capitula present, occasionally 2–4 coalescing into a syncephalum or forming a congested inflorescence.

Collections: 89 collections were examined, predominantly from the north desert areas of Libya and Egypt.

b. Subsp. **cyrtolepidioides** (Pomel) Humphries, **stat. nov.**

Anacyclus cyrtolepidioides Pomel, *Nouv. Mat. Fl. Atl.* : 54 (1874). Orig. coll.: *Kralik* 248, Gabes (BM, E, G, LE, Z, isotypi).
Anacyclus valentinus sensu Desf., *Fl. Atl.* **2** : 285 (1799) sphalm., non. L.
Cyrtolepis monanthos Less. in *Linnaea* **6** : 166 (1831).
Anacyclus mauritanicus Pomel, *Nouv. Mat. Fl. Atl.* : 55 (1874). Orig. coll.: *Pomel s.n.* Hautes steppes et montagnes des Ksous Mkraoula, El Beida, Aflou, Ksel (AL, holotypus; MPU, isotypus).

Anacyclus alexandrinus Boiss. in Batt. & Trabut, *Fl. Algér.* **3** : 452 (1890) sphalm, non Willd.
Anacyclus valentinus var. *tripolitanus* Borzi & Matthei in *Boll. Soc. bot. ital.* **1913** : 139 (1913).
Anacyclus cyrtolepidioides var. *mauritanicus* (Pomel) Batt. ex Jahandiez & Maire, Cat. *Pl. Maroc* **3** : 767 (1934).

Illustration: Gubb, 1913 : tab. 12.

Common names: Djerf, Sorret el Kebch, Rebiana.

Peduncles decumbent, emerging from a reduced, branched central stem, slender. Central capitulum absent.

Collections: 48 collections were examined, predominantly from Tunisia and Algeria.

3. **Anacyclus maroccanus** (Ball) Ball

in *J. Linn. Soc.* (Bot.) **16** : 504 (1878).
Anacyclus clavatus subsp. *maroccanus* Ball in *J. Bot. Lond.* **11** : 365 (1873). Orig. coll.: *J. Ball. s.n.* (31 May, 1871), ex provincia Shedma juxta Mskala, Insturia, Agadir, Marrakesh (K, holotypus, BM, LE, P).
Anacyclus valentinus var. *maroccanus* Ball ex Pitard, *Expl. Sci. Maroc. Bot.* **1** : 57 (1913), *nom. nud.*

Illustrations: Figs 2, 4, 16.

Common names: Chemt-el-fellous.

Annual; main stems extremely short, 1–2 cm long, or virtually absent, emerging from a simple taproot. *Leaves* alternate, sessile, oblong to spathulate in outline, 2·0–10·0 × 0·5–2·5 cm, tri-pinnatisect, sparsely to densely villous, especially when young. Primary lobes in 7–12 subopposite or alternate pairs, reduced at the base; ultimate segments long-acuminate; rhachis prominent, long-cuneate, broad at the base. *Inflorescence* a very contracted corymbose cyme; peduncles 2–12 erect, conspicuously spreading or decumbent, (2·0–) 5·0–30 cm long, emerging spirally from the axils of the stem leaves or basal rosette, ± glabrous to densely villous (especially towards the apex) and often tinged with red, distinctly clavate, up to 6·0 mm wide but narrowing slightly immediately below the capitulum. *Involucre* 5·0–12·0 (–15·0) mm; involucral bracts multiseriate 4·0–6·0 × *c.* 0·2 mm, triangular, herbaceous, green with a thin dark-brown margin, somewhat erose at the apex; receptacular scales ± oblong to obcuneate, 2·5–3·5 × 2·5–3·5 mm with tough, chartaceous centres and thinner, membranous wings, the apex cuspidate. *Ray-florets* white with a deep red stripe below; ligule 7·0–26·0 mm × 2·5–5·0 mm, usually minutely 3-lobed at the apex; tube 3·0–4·0 × *c.* 0·5 mm, anterior-dorsally compressed with a narrow, winged margin *Disc-florets* 3–4 × 0·5–0·7 mm, anterior-dorsally compressed with narrow winged margins; lobes narrow-triangular, cucullate, with extended heads on two of the lobes. *Styles c.* 3·5 mm long, style arms 0·5–0·8 mm long. *Stamens* 3·0–3·5 mm, anthers 1·5–2·0 mm. *Cypselas* 2·0–2·6 × 0·9–1·8 mm, obcuneate; wings 0·2–0·5 mm wide, thin, crenate, with two minute auricules; epicarp pale brown-grey, covered with long, longitudinally orientated myxogenic cells. *Pappus* either a minute crenate corona or occasionally absent.

Flowering period: Mainly March–April.

Observations: This distinctive species is generally a creeping or decumbent annual, with a markedly reduced main stem. Superficially, the habit and the white ligules with a red stripe of *Anacyclus maroccanus* are similar to *A. pyrethrum*. However, the fruit structure is entirely different, the crenate margins being similar to those of *A. monanthos*.

Distribution and ecology: See Fig. 13. An ephemeral annual of the Moroccan plain. Generally restricted to roadside habitats.

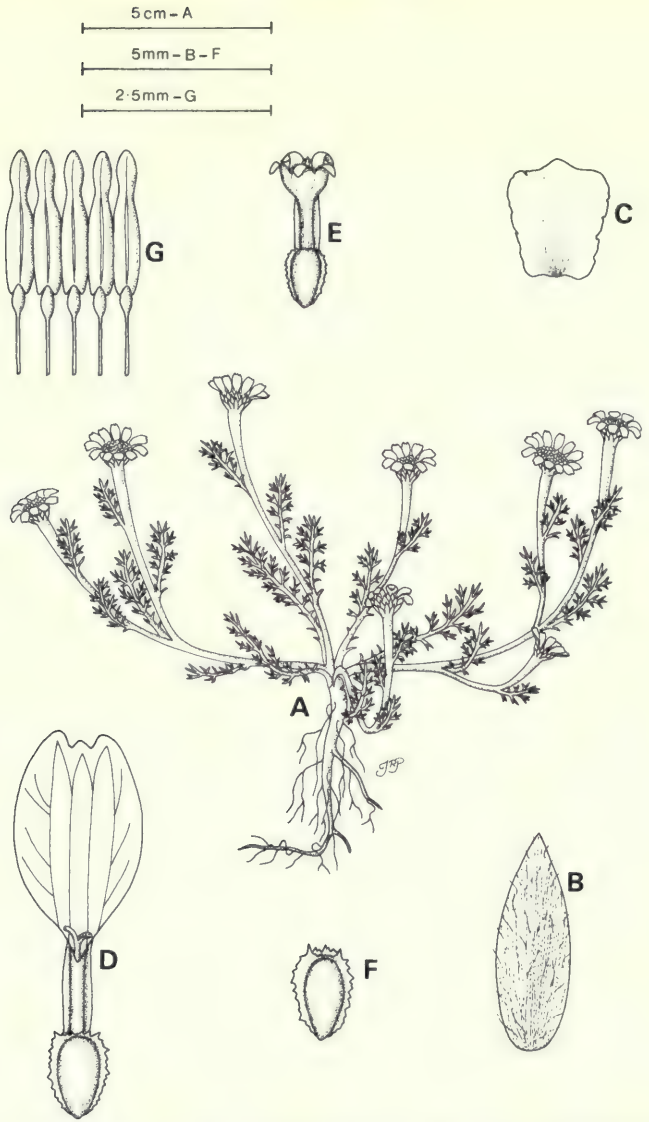


Fig. 16 *Anacyclus maroccanus*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

Collections: 43 collections examined from the north-western plain of Morocco.

4. **Anacyclus radiatus** Loisel.

Fl. Gall. : 583 (1807). Orig. coll.: Herb. Loiseleur des Longchamps, 'Environs d'Hières (leg.) par M. Leon Dufour etc.' (AV, lectotypus).

Anthemis valentina L., *Sp. Pl.* : 895 (1753). Orig. coll.: Herb Cliff. '*Chrysanthemum folio matricariae latiori, flore aureo*' (BM, lectotypus).

Chamaemelum valentinum (L.) All., *Fl. Pedem.* **1** : 187 (1785).

Common names: Yellow Anacyclus.

Annual or short-lived biennial; stems erect, simple, 7·0–12·0 cm high, emerging from a vestigial basal rosette, glabrous or hairy, often tinged with red. *Leaves* alternate, sessile, crowded at the

base, spathulate in outline, (2·5–) 4·0–16·0 × 2·0–5·0 cm, tripinnatisect; primary lobes in 6–14 subopposite or alternate pairs, reduced at the base; ultimate lobes short, simple, acuminate; rhachis broad, flattened at the base, slightly decurrent. *Inflorescence* a corymbose cyme; peduncles terminal, often clavate, hollow and up to 5 mm wide at the apex. *Involucre* (5·0–) 15·0–18·0 mm; involucral bracts in 2 or 3 rows; outer bracts triangular to linear-oblong, herbaceous, with a thin brown erose scarious margin; inner bracts oblong-obovate to spathulate, (4–) 5–8 × 1·5–3·0 mm, chartaceous, with a thin flabelliform laciniate membranous apex; receptacular scales 3·5–5·0 × 2·0–3·0 mm, chartaceous, obcuneate, mucronate, somewhat inwardly curved. *Ray florets* (4–) 8·0–17·0 (–22) mm long × (0·8–) 2·5–7·0 (–10·0) mm wide, yellow, cream or white, sometimes with a red-purple stripe below, ± truncate, shallowly emarginate to 3-lobed at the apex; tube 3·5–4·0 × 0·6–1·5 mm, anterior-dorsally compressed, with distinct, parallel-sided lateral wings. *Disc florets* 3·0–4·5 mm long, tube 0·3–1·4 mm wide, hypocrateriform; lobes triangular-ovate, acute, usually regularly cucullate, or with extended hoods on 2 of the lobes. *Styles* 3·0–4·0 mm, style arms *c.* 0·8 mm long. *Stamens* 3·4–3·8 mm, anthers *c.* 0·5 mm. *Cypselas* 2·5–4·0 × 1·0–3·0 (–3·8) mm, widely obovate to obcuneate, pale brown, covered with short, longitudinally orientated, striate myxogenic cells; lateral wings tough, hyaline when mature, 0·4–0·8 (–1·0) mm wide, terminating in an erect or slightly inwardly projecting point. *Pappus* a fimbriate corona, contiguous with the lateral wings, abaxially deeply emarginate to sometimes completely absent on the inner disc florets.

Flowering period: Mainly March–September; although occasional flowering specimens have also been recorded for January, February and October.

Chromosome number: 2n = 18.

Variation: Anacyclus radiatus is a robust annual herb easily distinguished from other species by the inner spathulate involucral bracts with expanded, membranous erose, hyaline apices. It is widespread over the western Mediterranean region and varies along the distribution range. As indicated by ligule colour it forms two fairly discrete taxa with distinct geographical distribution. Subsp. *radiatus*, found in north-west Morocco, the Atlantic coast of Portugal and the Mediterranean coasts of Algeria, Libya, France, Spain and Italy, and introduced in the eastern Mediterranean, is unique within the genus by the possession of yellow ligules (the remainder being white or rayless). In southern Morocco around the regions of Oueds Sous and Massa, the Sous valley towards Taroudant and in the Canary Islands, the white-rayed forms of subsp. *coronatus* completely replace subsp. *radiatus*. In various Atlantic coast localities of Morocco from Safi to Mogador there are several populations exhibiting intermediates between the two subspecies. Populations with pale yellow ligules have been called var. *ochroleucus* Ball. Various other colour morphs exist, particularly sulphur yellow forms known as var. *sulfureus* Braun-Blanquet & Maire and an unnamed form with pale yellow or whitish straps and deep yellow bases to the ray florets, which also occur in this region. None of these forms really warrants formal status. Both subspecies have sporadic individuals with red stripes on the lower side of the ligule (a plesiomorphous condition shared by *A. pyrethrum* and *A. maroccanus*), which for subsp. *radiatus* have been called *A. purpurascens* (Pers.) DC. or subvar. *purpurascens* (Pers.) Rouy.

In his protologue, Murbeck distinguishes subsp. *coronatus* (as a variety) not only by ligule colour but also by pappus shape: '. . . in facie interna pappo magno continuo lacero-fimbriato praeditis'. Although all material of this subspecies does seem to have an extremely large fimbriate pappus, the character is not restricted to this taxon but is also very common in individuals with yellow ray florets, particularly in northern Morocco and southern France.

Distribution and ecology: See Fig. 18. *Anacyclus radiatus* occupies a considerable area in lowland localities of the western Mediterranean from Ifni and the Canary Islands in the south to south central France and Italy in the north. Subsp. *radiatus* follows the coast and roadsides from Mogador in the south to around Tangier in north Morocco, occurring also inland around Fez.

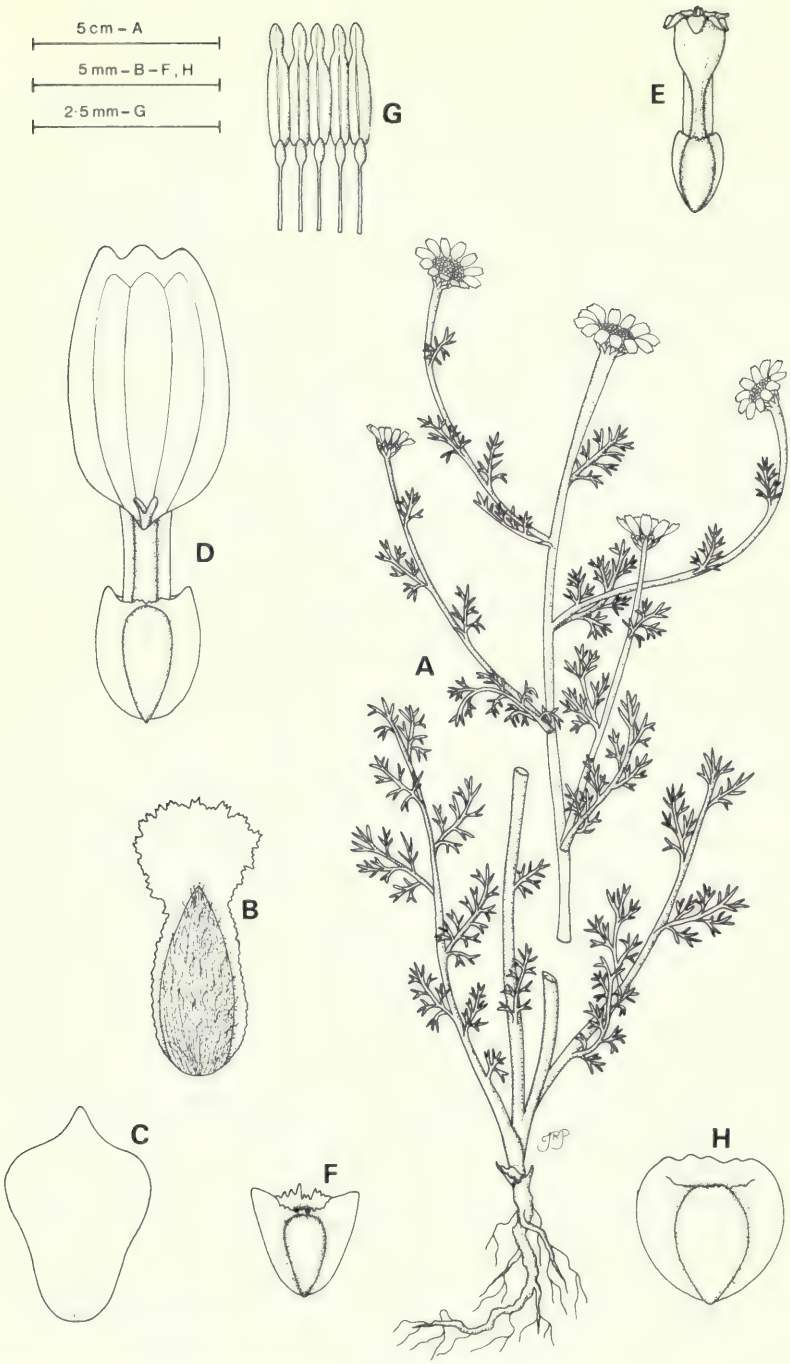


Fig. 17 *Anacyclus radiatus* subsp. *radiatus*: A – habit, B – inner involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers. Subsp. *coronatus*: H – cypsela.

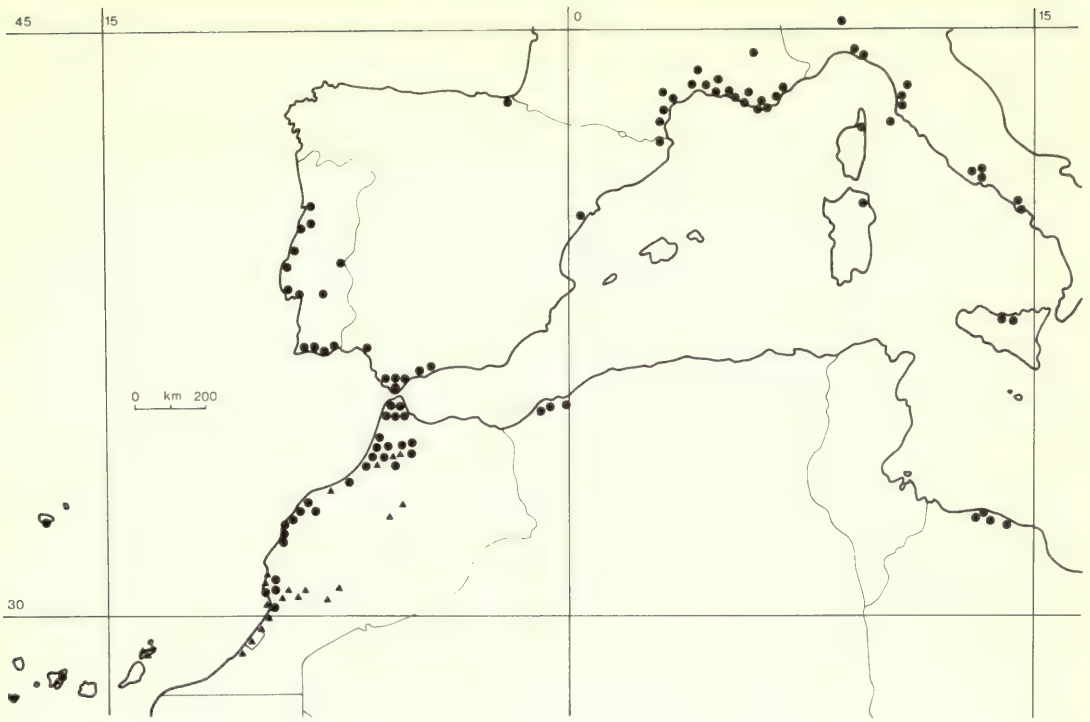


Fig. 18 Distribution of *Anacyclus radiatus* subsp. *radiatus* (●) and subsp. *coronatus* (▲).

Isolated collections have also been made from coastal regions around Oran in Algeria and Tripoli in Libya. Its European distribution is confined almost entirely to warm coastal places and around towns in Portugal, Spain, France, Italy, Sicily, Corsica and Sardinia. Subsp. *coronatus* occurs only in Morocco and the Canary Islands. It occurs most commonly in the Sous valley between the Haut Atlas and Anti-Atlas mountains, but occasional collections have been obtained as far north as the Marmora forest near Rabat.

Subsp. *radiatus* is mostly a ruderal of disturbed cultivated land but occurs on sand dunes and other shifting habitats in coastal localities. Subsp. *coronatus* occurs mostly on dry sandy soil or sand dunes, particularly in dried-up waddis.

a. Subsp. **radiatus**

Anacyclus aureus sensu Brot., *Fl. Lusit.* **1** : 363 (1804); DC. in Lam. *Fl. Fr.* **4** : 202, tab. 700, fig. 2 (1805) *pro parte quoad basionym.*
Anacyclus aureus (var.) β *radiatus* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in herb. Lugd. Bat. 900, 68–129 (L, lectotypus).
Anacyclus valentinus (var.) * (α) *bicolor* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in herb. Lugd. Bat. 900, 68–128 (L, lectotypus).
Anacyclus valentinus (var.) β *purpurascens* Pers., *Syn. Pl.* **2** : 465 (1807). Orig. coll.: Herb. Persoon in Herb. Lugd. Bat. 900, 68–137, Montpellier ad mare (L, lectotypus).
Anacyclus purpurascens (Pers.) DC. in Lam., *Fl. Fr.* **5** : 481 (1815).
Hiorthia aurea (L.) Less., *Syn. Gen. Comp.* : 258 (1832), *pro parte quoad basionym.*
Anacyclus radiatus (var.) β *purpurascens* (Pers.) DC. *Prodr.* **6** : 16 (1838).
Anacyclus pallescens Guss., *Fl. Sic. Syn.* **2** : 494 (1844). Orig. coll.: *Gussone s.n.* In herbosis maritimis Cefalu alla marina (Gasparrini) (not seen).
Anacyclus radiatus (var.) γ *pallescens* (Guss.) Arcangeli, *Comp. Fl. Ital.* : 359 (1882).
Anacyclus radiatus subvar. *purpurascens* (Pers.) Rouy, *Fl. Fr.* **8** : 239 (1903).
Anacyclus radiatus var. *sulfureus* Braun-Blanquet & Maire, in *Mém. Soc. Sci. nat. Phys. Maroc* **8** : 232

(1924) Orig. coll.: *Braun-Blanquet & Maire s.n.*(1921), Grande Île de Mogador. Pâturages sablonneux entre Tiflet et Camp Monod (AL, holotypus).

Anacyclus radiatus var. *typicus* Fiori, *Nuov. Fl. Anal. Ital.* **4** (2) : 650 (1927), *nom. illegit.*

Anacyclus radiatus var. *typicus* subvar. *concolor* Maire in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 766 (1932), *nom. nud.*

Illustrations: Figs 2, 4, 17. Miller, 1760 : tab. 73; Reichenbach, 1854 : tab. 999, fig. III, 12–14; Cesati, Passer & Gibelli, 1867–86 : tab. 79, figs 5 b–e; Cusin & Ansberque, 1873 : tabs 147, 148; Regel 1882: tab. 1074; Coste, 1903 : p. 348, fig. 1961; Fiori & Paoletti, 1904 : 426; Cadevall & Sallent, 1917 : p. 278, fig. 1422; Bonnier, 1922 : tab. 297, fig. 1474; Bouloumoy, 1930 : tab. 217, fig. 4; Post, 1933 : p. 58, fig. 426; Nègre, 1962 : p. 285, tab. 124; Zhangeri, 1976 : tab. 143, figs 5237, 5239, 5240; Haslam, Sell & Wolseley, 1977 : tab. 45.

Common names: El-Guentouss, Marguerite des Doukkala.

Ligules yellow, or yellow with a red stripe below. Pappus 0·2–0·5 (–1·0) mm long on anterior, (adaxial) face.

Collections: 329 collections, predominantly from Spain, Morocco and France.

b. Subsp. **coronatus** (Murb.) Humphries, **stat. nov.**

Anacyclus radiatus var. *coronatus* Murb., *Contr. Fl. Maroc* **2** : 55 (1923). Orig. coll.: *Ibrahim* (20 May 1889), Oued Tizi (LD, lectotypus, LE).

Anacyclus radiatus var. *ochroleucus* Ball in *J. Linn. Soc.* (Bot.) **16** : 504 (1878). Orig. coll.: *Lowe s.n.* in arenosis maritimus prope Mogador (K, holotypus).

Anacyclus exalatus Murb. in *Bot. Notiser* **1923**: 61 (1923); *Contr. Fl. Maroc* **2**: 55 (1923). Orig. coll.: *Ibrahim s.n.* (June, 1877), in herb. Cosson, prope oppidum Agadir imperii maroccani meridion alis (LD, lectotypus).

Anacyclus medians Murb. in *Bot. Notiser* **1923** : 60 (1923); *Contr. Fl. Maroc* **2**: 53 (1923). Orig. coll.: *Murbeck s.n.* (23 April 1931), in herbosis ad Aguedal prope urbem Marrakech (LD, holotypus, MPU).

Anacyclus submedians Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **15** : 39 (1927). Orig. coll: *Maire s.n.* (24 April 1925), Hab. in arvis argillaceo-humosis humidis planitei Gharb prope Sidi-Yaya, ubi martio et aprili floret (AL, holotypus, RAB, P, MPU).

Anacyclus ifniensis Caballero in *Trab. Mus. nac. Cienc. nat. Madr.* (Bot.) **28** : 24 (1935). Orig. coll.: *Caballero s.n.* (16 June 1934), en la plana de Ifni (M, holotypus, MPU).

Anacyclus ifniensis forma *viridis* Caballero, in *Trab. Mus. nac. Cienc. nat. Madr.* (Bot.) **28** : 25 (1935). Orig. coll.: *Caballero s.n.* (17 June, 1934), in umbrosis marginum flumine Ifni (M, holotypus).

Anacyclus radiatus var. *coronatus* Murb. subvar. *discolor* Maire in *Bull. Soc. Hist. nat. Afr. N.* **26** : 211 (1935). Orig. coll.: *Maire & Wilzeck s.n.* (1 April 1934), sables maritimes près du Cap Ghir (AL, holotypus, RAB, P).

Illustrations: Murbeck, 1923 : p. 54, figs a–h.

Ligules white, or rarely white with a red stripe below. Pappus (0·3–) 0·5–1·2 mm long on anterior (adaxial) face.

Collections: 51 collections, particularly from the Sous valley in south-west Morocco and Lanzarote in the Canary Islands.

5. **Anacyclus clavatus** (Desf.) Pers.

Syn. Pl. **2** : 465 (1807).

Anthemis clavata Desf., *Fl. Atl.* **2** : 287 (1799). Orig. coll.: Herb. Desf. (P, holotypus).

Anthemis tomentosa sensu Gouan, *Obs. Bot.* : 70 (1773), *pro parte quoad holotypus autem non L.* (= *Anthemis*).

Chamaemelum tomentosum sensu All., *Fl. Pedem.* **1** : 184 (1785).

Anthemis pedunculata Desf., *Fl. Atl.* **2** : 288 (1799). Orig. coll.: Herb. Desf. (P, holotypus).

Anthemis pubescens Willd., *Sp. Pl.* **3** (3) : 2177 (1800). Orig. coll.: Herb. Willd. 16246 (B, holotypus).
Anthemis biaristata DC. in Lam., *Fl. Fr.* **4** : 204 (1805); *Biv. Pl. Sic. Cent.* **2** : 7 (1807). Orig. coll.: Herb. DC., 'biaristata, les champs N.' (G–DC, holotypus).
Anacyclus pedunculatus (Desf.) Pers., *Syn. Pl.* **2** : (1807), *pro parte quoad basionym.*
Chamaemelum inodorum sensu Cup., *Pamph.* **2** : t. 69 (1807), non Vis.
Anacyclus divaricatus Cav. ex Balbis *Cat. Hort. Taur.* : 11 (1813); Steudel, *Nomencl. Bot.* 1st ed.: 41 (1821), *nom. nud.*
Anacyclus tomentosus sensu DC. in Lam., *Fl. Fr.* **5** : 481 (1815).
Chamaemelum incrassatum Hoffmanns. & Link, *Fl. Port.* **2** : 348 (1820). Orig. coll.: 'Frequent sur le bord de la rivière du Nabao près de Thomar' (? typus destructus).
Anthemis incrassata (Hoffmanns. & Link) Link, *Enum. Hort. Berol. Alt.* **2** : 345 (1822).
Anacyclus pubescens (Willd.) Reichb., *Fl. Germ. Excurs.* **2** : 225 (1831).
Bambagella clavata (Desf.) Ten., *Fl. Nap.* **5** : 235 (1835).
Anacyclus mucronulatus Hort. ex Steudel, *Nomencl. Bot.*, 2nd ed. : 82 (1840) *nom. nud., non* Guss.
Anacyclus tomentosus var. β *marginatus* Guss., *Fl. Sic. Syn.* **2** (1); 495 (1844), *nom. illeg.*
Anacyclus candolii Nyman, *Syll.* : 8 (1854).
Anacyclus aristulatus Link ex Nyman, *Consp.* **2** : 363 (1879), *nom. nud.*
Anacyclus clavatus var. α *typicus* Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1904), *nom. illeg.*
Anacyclus clavatus var. β *tomentosus* (L.) Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1904).
Anacyclus tomentosus forma *glabrus* [sic] Huter, Porta & Rigo in Fiori, *Fl. Anal. Ital.* **3** : 261 (1904), *nom. nud. et illeg.*
Anacyclus capillifolius Maire in *Bull. Soc. Hist. nat. Afr. N.* **22** : 296 (1931). Orig. coll: *Font Quer & Maire s.n.* (25 June 1930) 'In Atlante rifano: in lapidosis calcareis montis Krâa, 1600 m' (MPU, holotypus).

Illustrations: Figs 2, 4, 19. Reichenbach, 1854 : tab. 999, fig. II, 4–11; Cesati, Passer & Gibelli, 1867–86; tab. 79, fig. 5a; Cusin & Ansberque, 1873 : tab. 146; Hoffman, 1894 : 269 fig. K; Acloque, 1894 : 374; Fiori & Paoletti, 1904 : tab. 426, fig. 3590; Merino, 1906 : 365; Lazaro é Ibiza, 1907 : 658; Adamović, 1911 : tab. 66 : Cadevall & Sallent, 1917 : p. 277, fig. 1421 ; Small, 1918 : p. 22, fig. K, M. : Bonnier, 1922 : tab. 297, fig. 1473 : Ponzo, 1927 : p. 563, fig. 24; Nègre, 1962 : p. 285, fig. 712 a–c: Zhangeri, 1976 : tab. 143 : figs 5238, 5241; Heywood & Humphries, 1977 : p. 865, fig. 7.

Common names: Rebiana, Beehibchou, Bouibicha, Bo Melal, Math-el-Djadja, Redjelet el Rh'orab, Oum-el-ali, White Anacyclus.

Annual; stems 7·0–30·0 (–40·0) cm, slender to stout, procumbent to erect, usually much branched from the base or branching from the middle, sparsely to densely appressed villous. *Leaves* (1·5–) 2·5–11·5 × (0·5–) –3·6 cm tri- to bipinnatisect, oblanceolate in outline, glabrescent to densely villous, usually sessile but occasionally long-petiolate; primary lobes in 3–12 subopposite or opposite pairs; ultimate segments linear-lanceolate 3·0–7·0 × *c.* 0·5 mm; rhachis flat, ± cuneate at the base with 3 or more prominent veins. *Inflorescence* a lax, corymbose cyme with up to 40 erect or ascending peduncles; peduncles markedly clavate near the apex at maturity, villous just below the capitulum. *Involucre* (0·5–) 8·0–1·8 mm in diameter, hemispherical; involucral bracts in three rows, 1·8–7·0 × 0·5–2·0 mm, outer series linear-triangular, inner series ± rectangular usually densely villous, pale brown or green and thicker towards the centre with thin, scarious, entire, pale yellow to dark brown margins; receptacular scales 1·7–5·0 × *c.* 2·5 mm, obovate or cuneate and mucronate, slightly caniculate towards the apex, somewhat membranous. *Ray florets* white; ligules dimorphic, 5·5–16·5 × 2·0–7·0 mm, white, trifid, usually somewhat rounded, creamy white; tube 3·5–5·5 × 0·5–1·0 mm, anterior-dorsally compressed with narrow, ± parallel-sided wings. *Disc florets* 3·5–5·0 × 0·5–1·3 mm, hypocrateriform with a distinct, campanulate corolla and a narrow basal tube; tubes anterior-dorsally compressed with broad, rounded wings towards the base, up to 1·0 mm wide in outer series, but narrower, *c.* 0·6 mm wide, towards the centre of the disc; lobes usually dimorphic, with three short lobes 0·5–0·6 mm long and two extended lobes, up to 2·0 mm long, especially towards the centre of the disc. *Styles* 3·0–4·0 mm long, style branches 0·3–0·6 mm long. *Stamens c.* 4·0 mm long, anthers 1·8–2·0 mm long. *Cypselas* (1·5–) 2·5–3·5 (–5·0) × (0·4) 1·5–4·7 mm, broadly obovate, those of the ray and outer disc with

Fig. 19 *Anacyclus clavatus*: A – habit, B – involucral bract, C – receptacular scale, D – capitulum, E – ray floret, F – disc floret, G – cypsela, H – anthers. *A.* × *valentinus*: I – capitulum, J – ray florets.

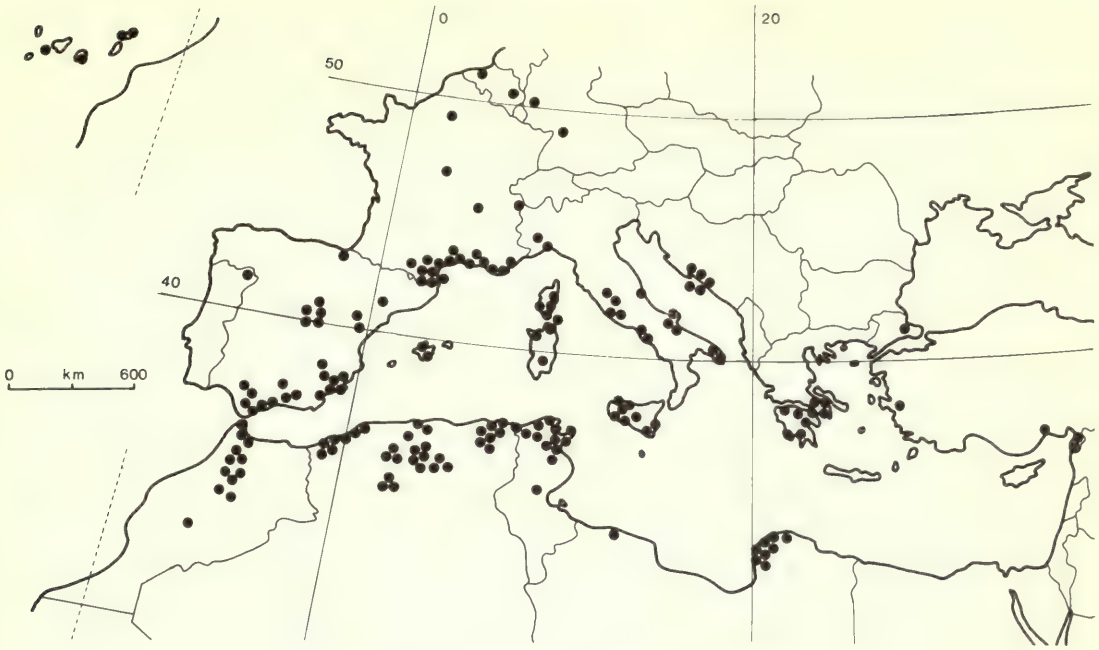


Fig. 20 Distribution of *Anacyclus clavatus*.

wings up to 1·2 mm, those from the centre of the disc with wings *c.* 0·3 mm in diameter, wings truncate or with bluntly pointed auricles. *Pappus* an anterior lacerate corona.

Flowering period: February–July.

Chromosome number: 2n = 18.

Observations: This species is most closely related to *Anacyclus homogamos* and *A. linearilobus*. They are similar in many respects, but *A. homogamos* can be readily distinguished by its generally smaller habit and hermaphrodite discoid capitula, and *A. linearilobus* by the greatly dissected leaves and longer spines on the receptacular scales.

Variation: *Anacyclus clavatus* varies considerably in habit, pubescence and ligule characters. As a consequence, different morphs have been given a variety of names. The name var. *tomentosus*, for example, is one of the most commonly used names, since many populations are densely pubescent. This character, as with habit and ligule length, is a continuously variable feature; so I find little reason to give formal taxonomic ranks to apparently distinctive populations.

Distribution and ecology: See Fig. 20. *Anacyclus clavatus* is a pernicious weed occupying a considerable range in Mediterranean Europe and Africa. It is a dominant plant in disturbed habitats of north Morocco, Algeria, Tunis and Libya and occurs abundantly in similar habitats in many coastal and inland places of Spain, France, Italy, Jugoslavia, Greece and Turkey. Also it often appears as a casual in various parts of Russia and northern Europe.

Collections: 386 collections have been examined, mainly from southern Europe and north Africa.

6. **Anacyclus homogamos** (Maire) Humphries, **comb. et stat. nov.**

Anacyclus valentinus subsp. *dissimilis* var. *homogamos* Maire in *Bull. Soc. Hist. nat. Afr. N.* **23** : 189–190 (1932). Orig. coll.: *Maire s.n.* (1929), 'In arvis et pascuis Imperii maroccani australis: prope

Tahanout ad radices Atlantis majoris it ditione Reraya, ad alt 900–1000 m' (RAB, holotypus, MPU, isotypus).

Anacyclus tomentosus (var.) c. *discoideus* Guss., *Fl. Sic. Syn.* : 495 (1844). Orig. coll.: *Gussone s.n.*, Italia Caltanisetta, Lentini Alicata (NAP, lectotypus) (not seen).

Anacyclus clavatus (var.) β *discoideus* Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865); Batt. & Trabut, *Fl. Algér.* : 452 (1890), *pro parte.*

Anacyclus valentinus sensu Briquet & Cavallier in Burnat, *Fl. Alp. Marit.* **6** : 165 (1916), non L.

Anacyclus dissimilis var. *australis* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929) Orig. coll.: *Maire* 654, 'Hab in alveis arenoso-limosis torrentium in montibus Hoggar. Saharae centralis, ad alt. 1200–1450 m' (AL, lectotypus, MPU).

Anacyclus valentinus subsp. *eu-valentinus* Thell. in Jahandiez & Maire, *Cat. Pl. Maroc* **3** : 767 (1934), *nom. nud.*

Anacyclus valentinus subsp. *dissimilis* sensu Nègre, *Fl. Maroc Aride* **2** : 284 (1962), *quoad descr.*

Illustrations: Figs 2, 4, 21. Gaertner, 1791 : tab. 165; Lamarck, 1798 : tab. 700. fig. 1; Jaume St-Hilaire, 1808 : tab. 27; Nègre, 1962 : tab. 124, fig. 713.

Common names: Guerthoufa.

Annual; stems 5·0–40·0 (–50·0) cm, slender, ascending to erect, usually branched from the base, sparsely to densely appressed villous. *Leaves* (1·0–) 4·0–9·0 (–13·0) × 0·3–4·0 cm. tri- to bipinnatisect oblong or oblanceolate to obovate in outline, usually hairy, sessile. *Inflorescence* a lax corymb, with erect or ascending peduncles, emerging from a short stem; peduncles usually clavate at maturity, usually villous just below the capitulum. *Involucre* 5·0–18·0 mm in diameter, hemispherical; involucral bracts multiseriate, 3·0–7·0 × 1·8–3·0 mm; outer series linear-triangular, inner series rectangular, usually villous towards the centre and apex, brown or pale greenish with a thin brown scarious margin. Receptacular scales 3·0–4·5 × 1·1–1·7 mm, obovate or cuneate and mucronate, slightly caniculate towards the apex, somewhat membranous. Capitula discoid, all florets monoecious discoid. *Florets* 2·5–4·6 mm long, hypocrateriform with a distinct campanulate upper part; tube slender, anterior-dorsally compressed with broad, rounded wings towards the base; wings up to 1·2 mm wide in the outer series, *c.* 0·7 mm wide towards the centre of the capitulum, lobes irregularly dimorphic, particularly in central florets with three short lobes, 0·3–0·9 mm long and 2 long lobes up to 1·6 mm long. *Styles c.* 4·0 mm long, style branches 0·2–0·5 mm long. *Stamens* 3·8–4·0 mm long, anthers 1–2 mm long. *Cypselas* 1·5–4·2 × 1·4–3·8 mm, broadly ovate, with thin membranous wings; wings somewhat heteromorphic, those of the outer series with broad wings 0·7–1·8 mm wide with rounded or slightly pointed diverging auricles, those of the inner series with narrow wings 0·4–0·6 mm wide and less prominent auricles. *Pappus* a fimbriate corona contiguous with the wings, particularly developed on the anterior side of the apex.

Flowering period: March–July.

Chromosome number: 2n = 18.

Observations: This species is easily recognized by its broad, more or less parallel-sided, cypsela wings and the somewhat rounded wings at the base of the corolla tube. It is very closely related to *Anacyclus clavatus* and is considered in this revision to be its sister-species (see p. 108). However, it is a much less robust species, the capitula are obviously discoid with homogamous hermaphrodite disc-florets, and the cypselas have more delicate, but broader wings.

Many apparently discoid specimens of *Anacyclus* have been identified as *A. valentinus* L. when in fact they are not homogamous discoid but heterogamous with structurally reduced female ligules in the outer floret series of the capitulum (Fig. 19). There seem to be two possible reasons for this phenomenon: (i) either the short-liguled forms represent an intermediate stage in the evolution of discoid monoecious forms from gynomonoecious radiate taxa or (ii) the short-liguled plants are hybrids between discoid and radiate taxa.

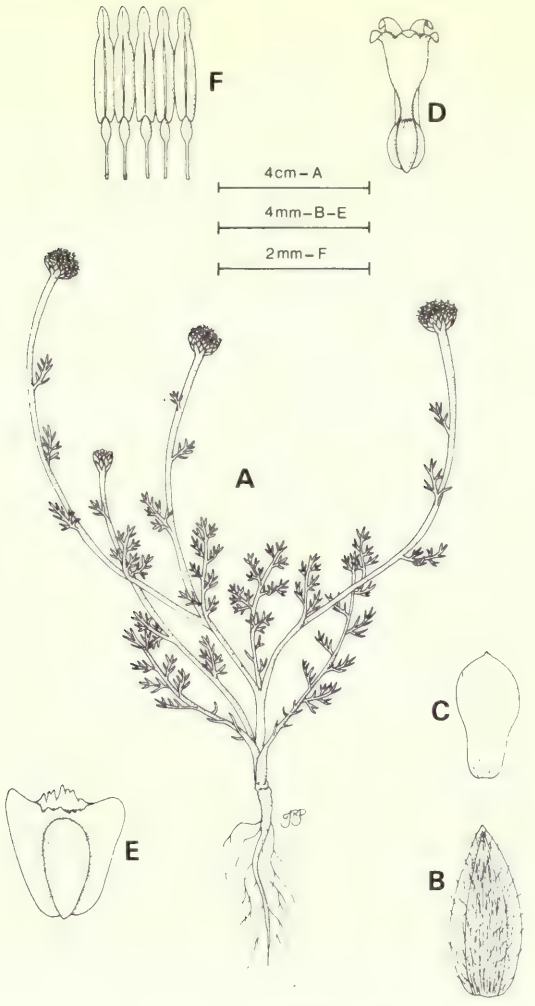


Fig. 21 *Anacyclus homogamos*: A – habit, B – involucral bract, C – receptacular scale, D – disc floret, E – cypsela, F – anthers.

The evidence will not be presented here since the details form part of a critical experimental study (Humphries, in press, *a*). However, the principal reasons for accepting the second hybrid hypothesis are that: (a) In almost all herbarium specimens, the ligules are extremely short and are frequently masked entirely by the involucral bracts. They fall into one particular size class and do not form a gradual series between rayed and rayless forms. There are fewer ligules in short-rayed morphs than can ever be found in a radiate plant, and these are irregularly arranged at the periphery of each capitulum. (b) This condition can readily be synthesized in artificial F_1 hybrids, especially in crosses involving *A. homogamos*, *A. clavatus* and *A. radiatus* (Humphries, in press, *a*). (c) In most herbarium specimens it is extremely difficult to identify ligule colour, but it is possible to show that in a number of cases both white and yellow short-rayed morphs exist. (d) The short-rayed plants are often found in mixed populations with the putative parents and invariably have sympatric distributions with one or both of them. (e) There are numerous citations in European literature (see synonyms) of collections believed to be rayless forms of *A. clavatus* and *A. radiatus* found in Europe. However, truly rayless forms are extremely rare in Europe and occur in abundance only in north Africa (Fig. 22).

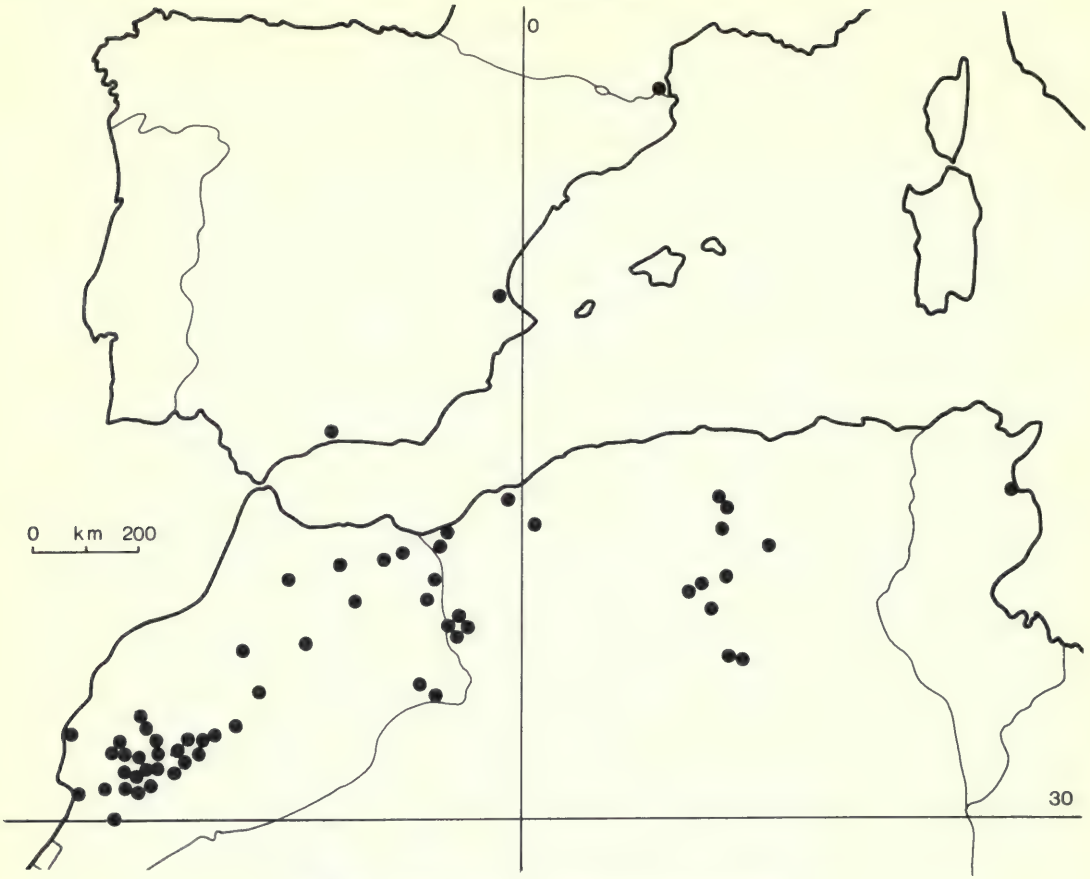


Fig. 22 Distribution of *Anacyclus homogamos*.

From these points it is possible to suggest that the short-rayed plants are established hybrids of *A. homogamos* × *radiatus* and *A. homogamos* × *clavatus*. Observations on habit and cypsela morphology support this interpretation, particularly in the variation of overall plant size, cypsela size, wing structure and auricle shape.

A. homogamos was not previously unrecognized but was considered to be only a variety of *A. valentinus* L. A new name had to be found for the homogamous plants, as Linnaeus's type for *A. valentinus* is a Spanish specimen of one of the hybrids *A. homogamos* × *radiatus* (see p. 109).

Collections: 75 collections were examined, mostly from Morocco.

a. **Anacyclus** × **inconstans** Pomel

Nouv. Mat. Fl. Alt. : 52 (1874).
(*A. homogamos* × *clavatus*). Orig. coll.: *Pomel s.n.*, Algeria Oued Dahra (MPU, holotypus).
Anacyclus clavatus var. *inconstans* (Pomel) Batt. & Trabut, *Fl. Algér* : 452 (1889); Fiori & Paol., *Fl. Anal Ital.* **3** : 261 (1903).

Illustrations: Small, 1918 : 22, fig. L.

Capitula incompletely radiate to apparently discoid, (5·0–) 10·0–22·0 mm in diameter. Outer florets ♀, ± tubular to truncate-ligulate, white, 2·0–3·0 (–11·0) mm long. Cypselas 3·0–4·0 × 2·0–4·0 mm, broadly ovate with thin, but broad-membranous wings with pointed to obtuse auricles.

b. **Anacyclus × valentinus** L.

Sp. Pl. : 892 (1753) (*A. homogamos* × *radiatus*). (Lectotypus, see p. 109).
Anacyclus lanuginosus Moench., *Meth.* : 581 (1794) Orig. coll.: typus destructus.
Anacyclus clavatus (var.) β *discoideus* Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865), *pro parte*.
Anacyclus valentinus (var.) β *microcephalus* Costa in Willk. & Lange, *Prodr. Fl. Hisp.* **2** : 84 (1865); Sennen in Sennen & Mauricio, *Cat. Fl. Rif. Or.* : 59 (1933). Orig. coll.: *Costa Pl.* catal exs. (M, holotypus) (not seen).
Anacyclus dissimilis Pomel, *Nouv. Fl. Atl.* : 53 (1874). Orig. coll.: *Pomel s.n.* (1 April 1862),Terrains Sablonneux du Sahara, Mzab, Metlili (A1, holotypus, MPU).
Anacyclus prostratus Pomel, *Nouv. Mat. Fl. Atl.* : 52–53 (1874). Orig. coll.: *Pomel s.n.*, 'Lieux herbeux des montagnes elevées d l'interieur (A1, holotypus) (not seen).
Anacyclus radiatus (var.) β *valentinus* (L.) Arcangeli, *Comp. Fl. Ital.* : 359 (1882).
Anacyclus radiatus (var.) β *discoideus* Chiov. in Fiori & Paol., *Fl. Anal. Ital.* **3** : 261 (1903) Orig. coll.: *Chiovenda*, 'Lit. del Lazio tra Furbana e S. Severa (FI, holotypus) (not seen).
Anacyclus valentinus var. *ligulata* Sennen in Anvari, *Jta Cienc. Nat. Barc.* **2** : 647 (1917), *nom. nud.*
Anacyclus valentinus subsp. *dissimilis* var. *typicus* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929), *nom. illeg.*
Anacyclus valentinus var. *eriolepis* Maire in *Bull. Soc. Hist. nat. Afr. N.* **20** : 186 (1929), *nom superfl.*
Anacyclus valentinus subsp. *dissimilis* (Pomel) Thell. in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 767 (1934).
Anacyclus valentinus subsp. *dissimilis* var. *eudissimilis* Maire in Jahandiez & Maire, *Cat. Pl. Maroc.* **3** : 767 (1934), *nom. illeg.*

Illustrations: Fig. 19 I, J. Schkuhr, 1808 : tab. 254 6; Reichenbach, 1854 : tab. 999, fig. 4; Cusin & Ansberque, 1873 : tab. 148 : Coste 1903 : 348; Cadevall & Sallent, 1917 : fig. 1423; Bonnier, 1922 : tab. 297, fig. 1475; Quezel & Santa, 1963 : tab. 975, fig. 2854.

Capitula apparently discoid or subradiate, 12·0–18·0 mm in diameter. Outer florets ♀, tubular to ligulate, yellow, 3·5–8·0 mm long. Cypselas *c.* 4·0 × 3·4 mm, obovate with broad wings and usually pointed auricles.

Hybrid collections (*Anacyclus* × *inconstans* and *A.* × *valentinus*): 171 collections, mostly from north Morocco, north Algeria and Spain.

Distribution and ecology: See Fig. 23. *Anacyclus homogamos* and its hybrids, *A.* × *inconstans* and *A.* × *valentinus*, are amongst the commonest roadside and field weed species of the western Mediterranean region, particularly in Morocco. The normal habitat is disturbed ground, especially in sandy and rocky places, particularly in montane regions of south-west Morocco but extending into north Morocco, Algeria, Tunisia and Spain.

It is not possible to demonstrate to any great extent, from herbarium material, the origin and spread of hybrids except to report that they have a sympatric distribution with either or both of the parental species. Along the eastern coast of Spain and the Mediterranean coast of France, some populations consist almost entirely of *A.* × *valentinus* L. Mixed populations of *A.* × *valentinus*, *A. clavatus* and *A. discoideus* occur around Oran in north-west Algeria, as is shown particularly by the collection of Faure, and in the Moyen Atlas Mountains, as is shown in the collections of Humphries, Jury, Mullin and Richardson.

7. **Anacyclus linearilobus** Boiss. & Reuter

Pugillus : 52 (1852). Orig. coll.: *Reuter s.n.*, Algér: Oran, inter la Stidia et Mostaganem in arenosis (G, holotypus).
Anacyclus acutilobus Durieu ex Boiss. & Reuter, *Pugillus* : 52 (1852). Orig. coll.: *Balansa* 689 (27 June 1852), Algér: Sables a voisinant la Batterie espagnole, pres d'Oran (MPU, holotypus, BM, C, E, G, K, LE, P).
Anacyclus rubricantes Durieu ex Boiss. & Reuter, *Pugillus* : 52 (1852).

Illustrations: Figs 2, 4, 24. Quezel & Santa, 1963 : 975, fig. 2853.

Fig. 23 Distribution of *Anacyclus* × *valentinus* (●) and *A.* × *inconstans* (▲).

Annual; stems 15·0–70·0 cm, erect, usually divaricately branching above, but occasionally from the axil of a 'rosette' leaf, rather striate, deep red, glabrous below to lightly pubescent above. *Leaves* 4·0–12·0 (–15·0) × 1·5–5·0 (–7·0) cm, ovate in outline, bi- to more rarely tripinnatisect, usually sessile above to long petiolate below; primary lobes in 4–9 opposite to subopposite pairs, with internodes up to 3 cm long; ultimate segments broad, acuminate, fleshy, rhachis narrow; peduncle leaves (bracts) 2–4·0 × 0·5–1·0 cm, pinnatisect, sessile, segments linear-acuminate. *Inflorescence* a lax, corymbose cyme, usually with 2–4 capitula; peduncles erect, branching from the middle of the stem, 7–23 cm long, distinctly clavate and hollow at the apex, pubescent (especially when young) to sometimes glabrous at maturity. *Involucre* 8·0–17·0 mm in diameter; involucral bracts in three rows, 4·5–7·0 × 1·5–2·5 mm, narrow-triangular to rectangular or ovate-oblong, acute, somewhat membranous, but with a thick, pale green to brown centre vein and narrow, scarious margins, invested with fairly long white hairs; receptacular scales 4·0–6·5 × 2·8–3·2 mm, obtrullate to narrowly obovate, cuspidate at the apex, with sharp spines at maturity, ± canaliculate above, flat below, usually pale-brown, glabrous. *Ray florets* white, reflexed at anthesis; ligules (5·0–) 8·0–16·0 × (3·0) 3·5–7·0 mm, acuminate to bifid, tube 1·8–2·5 × 1·0–1·3 mm, anterior-dorsally compressed, with broad ovate wings, female fertile. *Disc florets* 4·5–5·2 × *c.* 1·0 mm, infundibiliform, lobes ± equal in the outer series, but two distinctly longer than the rest in the inner series, wings broad, the basal part enlarged into an anterior circular appendage up to *c.* 1 mm wide, extending over the cypsela. *Styles* 3·5–3·8 mm long, branches 0·5–0·8 mm long. *Stamens* 3·5–4·0 mm long, anthers *c.* 1·8 mm long. *Cypselas* dimorphic, anterior dorsally compressed but subrectangular with thin hyaline wings, those of the ray florets broadly ovate, 3·5–4·0 × 3·0–3·5 mm, the wings with rounded auricles 1–1·3 mm wide, those of the disc florets

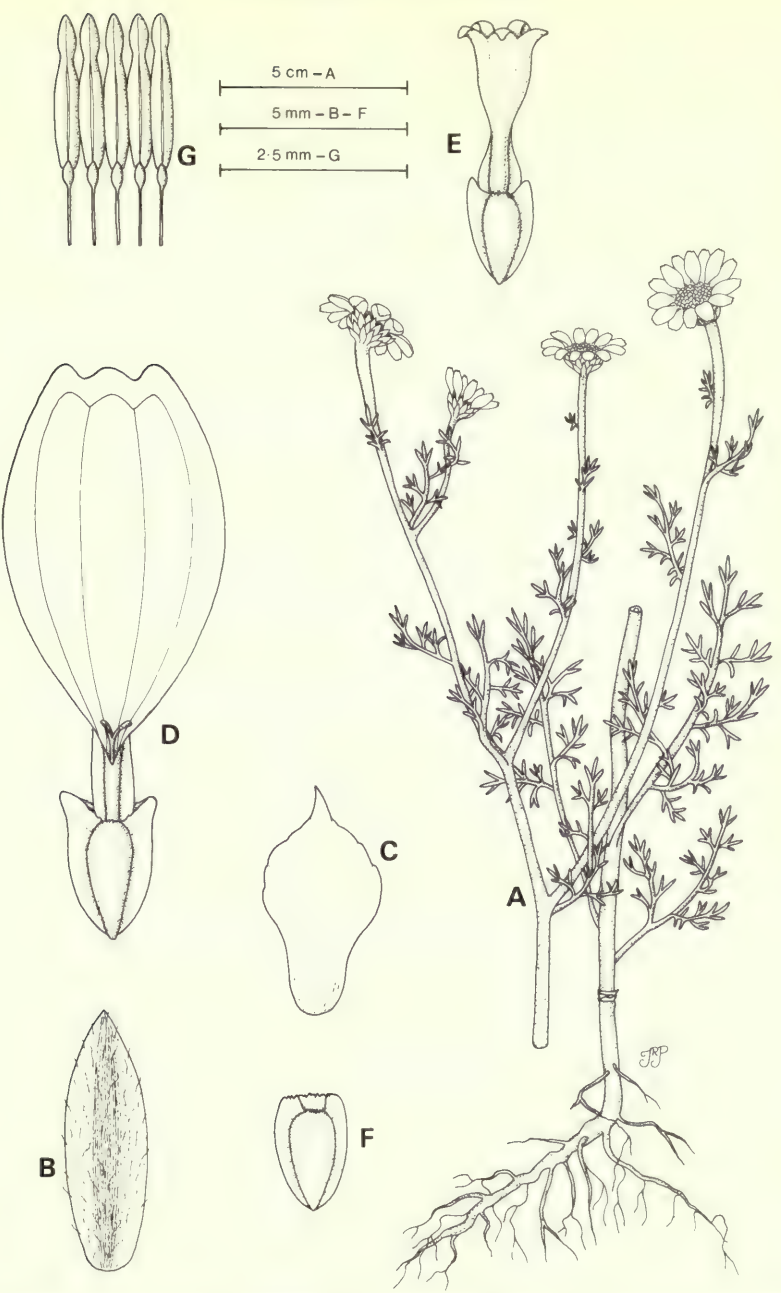


Fig. 24 *Anacyclus linearilobus*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret, F – cypsela, G – anthers.

obovate, 2·8–3·2 × 1·5–2·2 mm, with narrow truncate wings, 0·3–0·5 mm wide. *Pappus* a marginal corona or ± absent.

Flowering period: May–June.

Observations: This species is one of the most distinctive annuals in the genus, characterized by numerous vegetative and capitulum characters. The leaves are very fleshy, differing from the

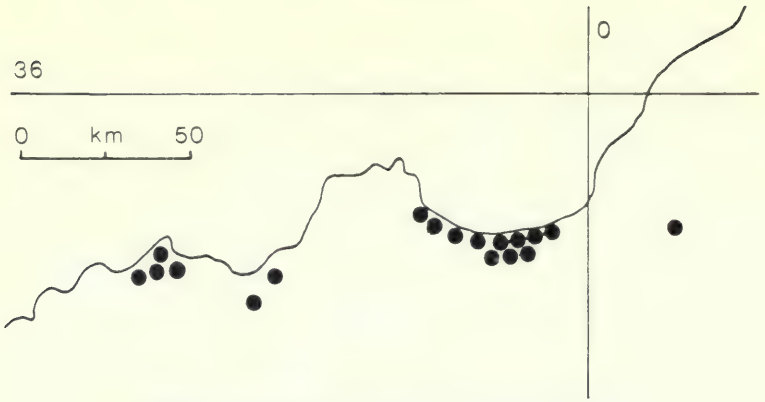


Fig. 25 Distribution of *Anacyclus linearilobus*.

closely related *Anacyclus clavatus* and *A. homogamos* by the wider internodes of the rhachis between the primary lobes, the broad fleshy retinate lobes, and the long red rhachis of the lower leaves. It shows an advanced disc corolla structure, similar to that of *A. nigellifolius*, where the lateral wings are expanded at the base into an anterior disc overlapping the cypsela, and is unique in the genus by the possession of long spiny receptacular scales.

Distribution and ecology: See Fig. 25. This species is endemic to Algeria. It grows on sand dunes and disturbed sandy ground up to about 50 m around Mostaganem, La Macta, Oran and Cap Falcon.

Collections: 30 collections were examined, all from coastal areas around Mostaganem, Oran and La Macta.

8. **Anacyclus latealatus** Hub.-Mor.

in *Feddes Reprium Spec. nov. veg.* **48** : 291 (1940). Orig. coll.: *A. Huber-Morath* 5664, Turkey: C2 Burdur zwischen Tefenni und Burdur, 18 Km nach Tefenni, 1100 (BASL, holotypus).

Illustrations: Huber-Morath, 1940 : tab. 327.

Annual; stems erect to ascending, up to 25 cm, divaricately branching from the base, often striate, tinged with red, sparsely villous to glabrescent. *Leaves* oblanceolate in outline, bipinnatisect, 2·0–4·0 × *c.* 1·0 cm, petiolate; primary lobes in 2–4 subopposite pairs; ultimate segments linear-lanceolate, 3·0–5·0 × *c.* 0·25 mm; rhachis narrow; peduncle leaves 2·0–3·0 × 0·5–1·0 cm, pinnatisect, often dilated at the base; segments linear. *Inflorescence* a protracted corymbose cyme; peduncles erect-ascending, 2·0–5·0 cm long only slightly thickened below the capitulum, ± densely villous. *Involucre* 10·0–13·0 mm in diameter, turbinate-hemispherical, involucral bracts in 3 rows 4·0–9·0 × 1·5–3·0 mm, lanceolate-acute, covered in dense white hairs, midrib green, apex and margins brown-scarious; receptacular scales lanceolate-acuminate, 7·0–8·0 × *c.* 1·5 mm, flat, hyaline, slightly green above, scarious, lightly villous. *Ray florets* white; ligules 8·0–9·0 × 2·0–3·0 mm, 2–3 lobed at the apex; tube 3·0–4·0 × *c.* 2·5 mm, anterior-dorsally compressed with very narrow wings, female fertile. *Disc florets* 3·0–4·0 × 2·5–3·0 mm, infudibuliform, lobes ± equal. *Styles c.* 3·5 mm long, branches *c.* 0·6 mm long. *Stamens c.* 4·0 mm long, anthers *c.* 1·8 mm long. *Cypselas* slightly dimorphic, broadly obovate (in disc florets) to obcuneate-auriculate (in ray florets), 4·0–6·0 × 5·0–8·0 mm, pale brown; lateral wings extremely thin, scarious, 2·5–2·75 mm wide, with pointed auricles. *Pappus* a fimbriate corona, contiguous with the auricles.

Flowering period: Virtually unknown, but flowering holotype was collected in June.

Observations: This species is easily recognized by its characteristic broadly winged, scarious cypselas. It can be distinguished from its sister-species, *Anacyclus nigellifolius*, by the truncate base of the corolla tube, the broader cypsela wings and the broad rhachis of the upper leaves.

Distribution and ecology: See Fig. 27. *Anacyclus latealatus* grows in fallow fields and steppic communities around 1100 m. It is known from only the south-west Turkish vilayet of Burdur. According to Grierson (1975) the species is endemic and probably Irano-Turanian.

Collections: Known only from the holotype.

9. **Anacyclus nigellifolius** Boiss.

Diagn. Pl. Or. I, **2** (11) : 13, t. 14 p. 267 (1849) ; Bois., *Fl. Or.* **3** : 322 (1875). Orig. coll.: *Haussknecht s.n.* (April 1867), Mesopotamia, in gracuis, Dara (G, holotypus, BM, JE, Z).
Anacyclus nigellifolius subsp. *orientalis* Grierson in *Notes R. bot. Gdn. Edinb.* **33** : 411 (1975) ; Grierson in Davis, *Fl. Turk.* **5** : 223 (1975). Orig coll.: *Sintenis* 817, Turkey: Urfa, Nemrut Dagh (LD, holotypus, BM).

Illustrations: Figs 2, 4, 26. Bouloumoy, 1930 : tab. 212, fig. 1; Davis, 1975 : 267, fig. 14, no. 13.

Annual; stems erect, slender, 10·0–20·0 cm long, simple or sparsely branched from, or above the middle, rarely much branched from below, ± glabrous. *Leaves* ± sessile, sparsely villous, bipinnatisect to pinnatisect, 1·5–3·0 × 0·3–1·5 cm; primary lobes in 5–6 subopposite pairs; ultimate segments 2·0–12·0 × 0·3–10 mm, acute; rhachis cuneate, thickened towards the base. *Inflorescence* monocephalic or a very loose corymbose cyme, peduncles usually emerging from or above the middle of the stem, clavate below the capitulum at maturity, distinctly villous above. *Involucre* 5·0–13·0 mm, turbinate-hemispherical; involucral bracts in three series, ovate acute in outer series to obovate obtuse in inner series, 4·5–7·0 × *c.* 2 mm, villous, distinctly centrally veined, green-brown towards apex, scarious, hyaline at the margin; receptacular scales obovate, acuminate, 5·0–7·0 × 2·0–2·8 mm, slightly caniculate, scarious, but thickened slightly above, glabrous. *Ray florets* white, ligule 4·5–6·0 × 1·0–3·0 mm, 2–3 fid; tube 3·5–4·8 × 1·0–1·2 mm, anterior-dorsally compressed with narrow wings, persistent at maturity. *Disc florets* 3·5–4·0 mm, base broadened into large circular appendage 2·5–3·0 mm wide covering top of cypsela on the anterior side, lobes equal. *Styles* 3·5–3·8 mm long, style branches 0·5–0·8 mm long. *Stamens* *c.* 4·0 mm, anthers 1·8–2·0 cm long. *Cypselas* ± monomorphic, somewhat rounded to obovate, 4·2–4·8 × 3·0–3·6 mm, pale brown; lateral wings extremely thin, transparent, scarious, 1·0–2·0 mm wide, with rounded auricles. *Pappus* coroniform to virtually absent, contiguous with wings.

Flowering period: May–June.

Observations: This species is similar in habit to *Anacyclus latealatus* and is its sister species, but it has more erect stems, less elaborate leaves, and rounded auricles on the cypselas. It differs from its congeners by the curious overlapping lobe at the base of the disc corollas, which is akin to that found in the monotypic *Leucocyclus formosus* Boiss., in which the two overlapping lobes clasp the top of the cypselas.

Variation: Stem size, stem branching, size of involucre and florets are subject to considerable variation. Grierson (1975*b*) distinguishes two subspecies, *nigellifolius* and *orientalis*, which differ in these characters, the generally more reduced form occurring in Hatay in southern Turkey. This variation, however, is continuous and not distinctly geographical, since plants with all the size-differences can be found in the Antilebanon, especially on Mount Hermon. The species is polymorphic, with each population differing slightly in genetic constitution. I do not think that this variation is worthy of taxonomic recognition.

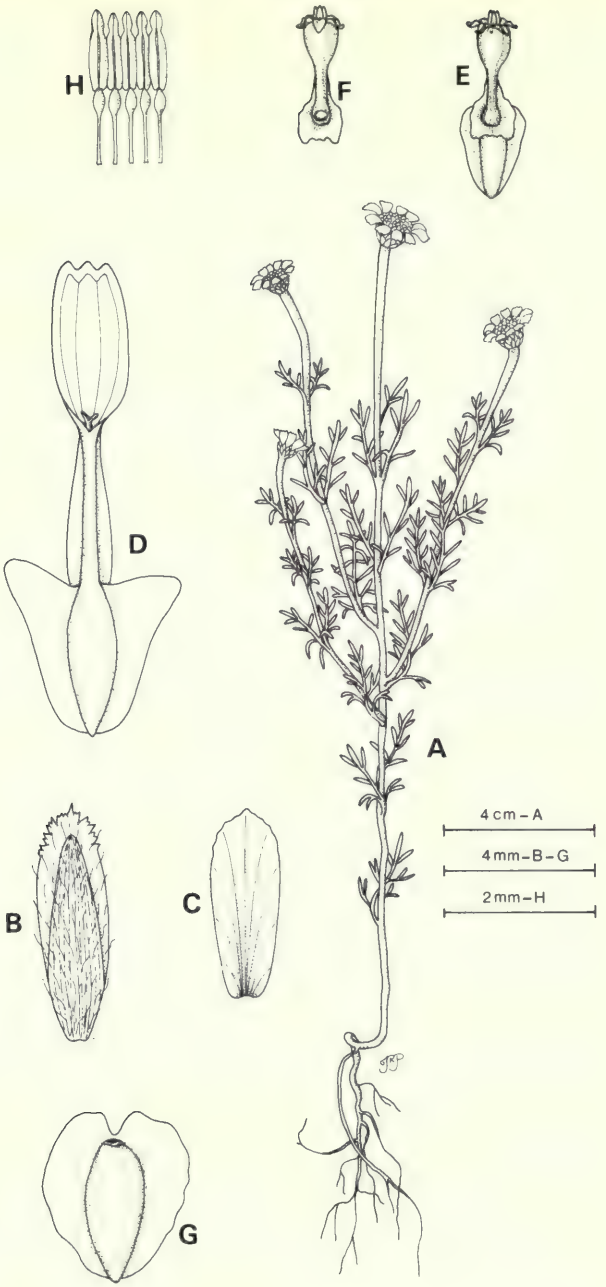


Fig. 26 *Anacyclus nigellifolius*: A – habit, B – involucral bract, C – receptacular scale, D – ray floret, E – disc floret (dorsal surface), F – disc floret (anterior surface), G – cypsela, H – anthers.

Distribution and ecology: Fig. 27. *Anacyclus nigellifolius* grows on rocky steppes and calcareous mountain slopes, between 1000 and 1500 m. It is restricted to the eastern Mediterranean region, from southern Anatolia and Syria to northern Iraq.

Collections: 18 collections were examined.

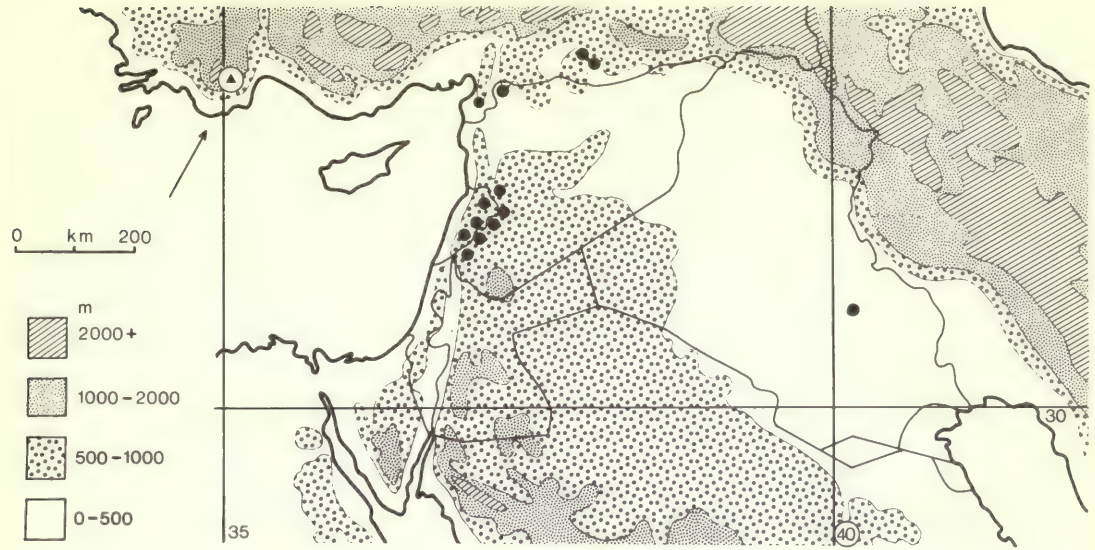


Fig. 27 Distribution of *Anacyclus nigellifolius* (●) and *A. latealatus* (▲).

Excluded taxa

Anacyclus sect. *Hiorthia* (Necker) DC., *Prodr.* **6** : 17 (1838).
altissimus (L.) G. Samp. in *Ann. Acad. Polyt. Port.* **14** : 162 (1920) = *Anthemis altissima* L.
anomalus Gay ex Boiss., *Fl. Or.* **3** : 283 (1875)= *Anthemis palestina* Reuter.
anthemoides (L.) Lag. ex Sprengel., *Syst. Veg.* **3** : 497 (1826)= *Anthemis abrotanifolia* (Willd.) Guss.
atlanticus Litard & Maire in *Mém. Soc. Sci. nat. Phys. Maroc* **4** (1) : 13 (1924)= *Heliocauta atlantica* (Litard & Maire) Humphries.
australis Sieber ex Sprengel, *Syst. Veg.* **3** : 497 (1826)= *Cotula australis* (Sieber ex Sprengel) Hook. f.
austriacus (Jacq.) G. Samp. in *Ann. Acad. Polyt. Port.* **14** : 162 (1920)= *Anthemis austriaca* Jacq.
barrelieri (Ten.) Guss., *Pl. Rar.* : 357 (1826)= *Achillea barrelieri* (Ten.) Schultz Bip.
ciliatus Trautv., in *Bull. Soc. Nat. Moscou* **41** (1) : 461 (1868)= *Anthemis ciliata* (Trautv.) Boiss.
creticus L., *Sp. Pl.* : 892 (1753)= *Anthemis rigida* (Sibth. & Sm.) Boiss. & Heldr.
formosus Fenzl ex Boiss., *Diag. Pl. Or. Nov.* II, **11** : 14 (1849)= *Leucocyclus formosus* Boiss.
inflatus Lehm. ex Steudel, *Nomencl. Bot.* 2nd ed. **1** : 82 (1840)= *Anthemis* sp.
membranacea Labill., *Icones Pl. Syr.* **3** : tab. 9 (1809)= *Leucocyclus formosus* Boiss.
mucronulatus (Bertol.) Guss., *Pl. Rar.* : 356 (1826)= *Achillea barrelieri* (Ten.) Schultz Bip.
nobilis L. ex Jackson, *Index Linn. Herb.* : 33 (1912)= *Chamaemelum nobile* (L.) All.
orientalis L., *Sp. Pl.* : 892 (1753)= *Anthemis orientalis* (L.) Degen.
pectinatus Bory & Chaub., *Nouv. Fl. Pelop.* : 59, tab. 30 (1838)= *Anthemis orientalis* (L.) Degen.
pyrethraria (L.) Sprengel, *Syst. Veg.* **3** : 497 (1826)= *Cotula pyrethraria* L.
tinctorius (L.) G. Samp. in *Ann. Acad. Polyt. Port.* **14**: 162 (1920)= *Anthemis tinctoria* L.
triumfetti (L.) G. Samp., in *Ann. Acad. Polyt. Port.* **14** : 162 (1920)= *Anthemis triumfetti* (L.) DC.
Hiorthia Necker, *Elem.* **1** : 97 (1790) pro parte= *Anthemis* L.
Lyonnetia Cass., *Dict. Sci. Nat.* : 102 (1825)= *Anthemis* L.

Acknowledgements

I would like to thank Mr A. Grierson for providing fruit material and photographs of *Anacyclus latealatus*, Mr. J. R. Press for drawing the maps and the species plates, Mrs M. Humphries for typing the manuscript, and Dr Kåre Bremer and Mr A. O. Chater for helpful comments and discussion.

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